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THE ECOLOGY OF THE MANGROVES OF SOUTH FLORIDA: A COMMUNITY PROFILE

by

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PREFACE

This profile of the mangrove community of south Florida is one in a series of community profiles which treat coastal and marine habitats important to man. The obvious work that mangrove communities do for man includes the stabilization and protection of shorelines; the creation and maintenance of habitat for a great number of animals, many of which are either endangered or have commercial value; and the provision of the basis of a food web whose final products include a seafood smorgasbord of oysters, crabs, lobsters, shrimp, and fish. Less tangible but equally important benefits include wilderness, aesthetic and life support considerations.

The information on these pages can give a basic understanding of the mangrove community and its role in the regional ecosystem of south Florida. The primary geographic area covered lies along the coast between Cape Canaveral on the east and Tarpon Springs on the west. References are provided for those seeking in-depth treatment of a specific facet of mangrove ecology. The format, style, and level of presentation make this synthesis report adaptable to a diversity of needs such as the preparation of environmental assessment reports, supplementary reading in marine science courses, and the development of a sense of the importance of this resource to those citizens who control its fate.

Any questions or comments about or requests for this publication should be directed to:

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CHAPTER 1. INTRODUCTION

1.1 "MANGROVE" DEFINITION

The term "mangrove" expresses two distinctly different concepts. One usage refers to halophytic species of trees and shrubs (halophyte = plant growing in saline soil). In this sense, mangrove is a catch-all, botanically diverse, non-taxonomic expression given to approximately 12 families and more than 50 species (Chapman 1970) of tropical trees and shrubs (see Waisel 1972 for a detailed list). While not necessarily closely related, all these plants are adapted to (1) loose, wet soils, (2) a saline habitat, (3) periodic tidal submergence, and (4) usually have degrees of viviparity of propagules (see section 2.3 for discussion of "viviparity" and "propagules").

The second usage of the term mangrove encompasses the entire plant community including individual mangrove species. Synonymous terms include tidal forest, tidal swamp forest, mangrove community, mangrove ecosystem, mangal (Macnae 1968), and mangrove swamp.

For consistency, in this publication we will use the word "mangrove" for individual kinds of trees; mangrove community, mangrove ecosystem or mangrove forest will represent the entire assemblage of "mangroves".

1.2 FACTORS CONTROLLING MANGROVE DISTRIBUTION

Four major factors appear to limit the distribution of mangroves and determine the extent of mangrove ecosystem development. These factors include (1) climate, (2) salt water, (3) tidal fluctuation, and (4) substrate.

Climate

Mangroves are tropical species and do not develop satisfactorily in regions where the annual average temperature is below 19°C or 66°F (Waisel 1972). Normally, they do not tolerate temperature fluctuations exceeding 10°C (18°F) or temperatures below freezing for any length of time. Certain species, for example, black mangrove, *Avicennia germinans*, on the northern coast of the Gulf of Mexico, maintain a semi-permanent shrub form by growing back from the roots after freeze damage.

Lugo and Zucca (1977) discuss the impact of low temperature stress on Florida mangroves. They found that mangrove communities respond to temperature stress by decreasing structural complexity (decreased tree height, decreased leaf area index, decreased leaf size, and increased tree density). They concluded that mangroves growing under conditions of high soil salinity stress are less tolerant of low temperatures. Presumably, other types of stress (e.g., pollutants, diking) could reduce the temperature tolerance of mangroves.

High water temperatures can also be limiting. McMillan (1971) reported that seedlings of black mangrove were killed by temperatures of 39° to 40°C (102° to 104°F) although established seedlings and trees were not damaged. To our knowledge, upper temperature tolerances for adult mangroves are not well known. We suspect that water temperatures in the range 42° to 45°C (107° to 113°F) may be limiting.

Salt Water

Mangroves are facultative halophytes, i.e., salt water is not a physical requirement (Bowman 1917; Egler 1948). In fact, most mangroves are capable of growing quite well in freshwater (Teas 1979). It is important to note, however, that mangrove ecosystems do not develop in strictly freshwater environments; salinity is important in reducing competition from other vascular plant species (Kuenzler 1974). See section 2.2 about salinity tolerance of mangrove species.

Tidal Fluctuation

While tidal influence is not a direct physiological requirement for mangroves, it plays an important indirect role. First, tidal stress (alternate wetting and drying), in combination with salinity, helps exclude most other vascular plants and thus reduces competition. Second, in certain locations, tides bring salt water up the estuary against the outward flow of freshwater and allow mangroves to become established well inland. Third, tides may transport nutrients and relatively clean water into mangrove ecosystems and export accumulations of organic carbon and reduced sulfur compounds. Fourth, in areas with high evaporation rates, the action of the tides helps to prevent soil salinities from reaching concentrations which might be lethal to mangroves. Fifth, tides aid in the dispersal of mangrove propagules and detritus.

Because of all of these factors, termed tidal subsidies by E.P. Odum (1971), mangrove ecosystems tend to reach their greatest development around the world in low-lying regions with relatively large tidal ranges. Other types of water fluctuation, e.g., seasonal variation in freshwater runoff from the Florida Everglades, can provide similar subsidies.

Substrate and Wave Energy

Mangroves grow best in depositional environments with low wave energy. High wave energy prevents establishment of propagules, destroys the relatively shallow mangrove root system and prevents the accumulation of fine sediments. The most productive mangrove ecosystems develop along deltaic coasts or in estuaries that have fine-grained muds composed of silt, clay and a high percentage of organic matter. Anaerobic sediments pose no problems for mangroves (see section 2.1) and exclude competing vascular plant species.

1.3 GEOGRAPHICAL DISTRIBUTION

Mangroves dominate approximately 75% of the world's tropical coastline between 25°N and 25°S latitude (McGill 1959). On the east coast of Africa, in Australia and in New Zealand, they extend 10° to 15° farther south (Kuenzler 1974) and in Japan, Florida, Bermuda, and the Red Sea they extend 5° to 7° farther north. These areas of extended range generally occur where oceanographic conditions move unusually warm water away from the equator.

Although certain regions such as the tropical Indo-Pacific have as many as 30 to 40 species of mangroves present, only three species are found in Florida: the red mangrove, *Rhizophora mangle*, the black mangrove, *Avicennia germinans*, and the white mangrove, *Laguncularia racemosa*. A fourth species, buttonwood, *Conocarpus erecta*, is not a true mangrove (no tendency to vivipary or root modification), but is an important species in the transition zone on the upland edge of mangrove ecosystems (Tomlinson 1980).

The ranges of mangrove species in Florida have fluctuated over the past several centuries in response to relatively short-term climatic change. Currently, the situation is as follows (Figure 1). The red mangrove and the white mangrove have been reported as far north as Cedar Key on the west coast of Florida (Rehm 1976) and north of the Ponce de Leon Inlet on the east coast (Teas 1977); both of these extremes lie at approximately 29°10' N latitude. Significant stands lie south of Cape Canaveral on the east coast and Tarpon Springs on the west coast. The black mangrove has been reported as far north as 30°N latitude on the east coast of Florida (Savage 1972) and as scattered shrubs along the north coast of the Gulf of Mexico.

Intertidal Distribution

The generalized distribution of the red and black mangrove in relation to the intertidal zone is shown in Figure 2a. Local variations and exceptions to this pattern occur commonly in response to localized differences in substrate type and elevation, rates of sea level rise, and a variety of other factors (see section 3.2 for a full discussion of mangrove

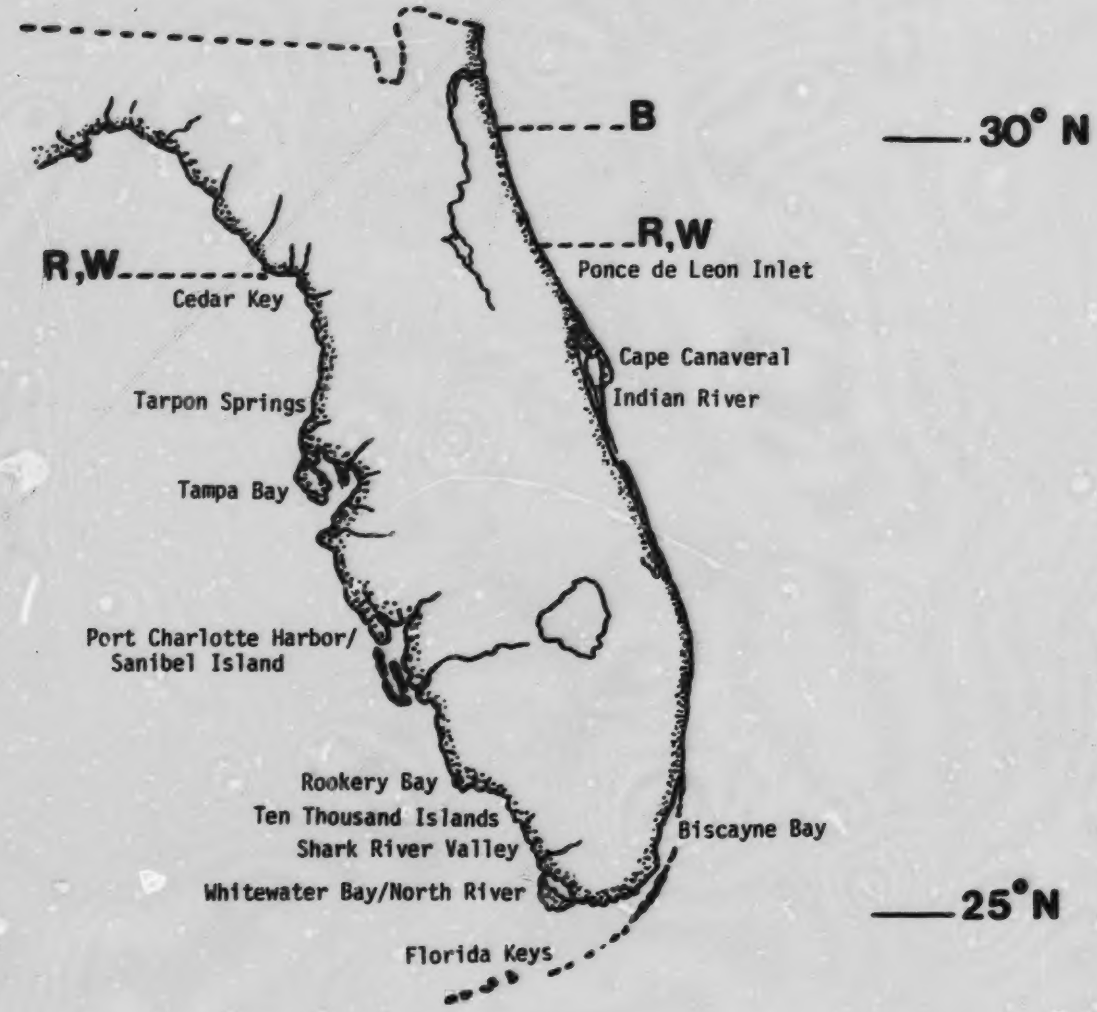

B
30° N
R,W
Ponce de Leon Inlet
R,W
Cedar Key
Cape Canaveral
Indian River
Tarpon Springs
Tampa Bay
Port Charlotte Harbor/
Sanibel Island
Rookery Bay
Ten Thousand Islands
Shark River Valley
Biscayne Bay
Whitewater Bay/North River
25°N
Florida Keys

Figure 1. Approximate northern limits for the red mangrove (R), black mangrove (B), and white mangrove (W) in Florida (based on Savage 1972); although not indicated in the figure, the black mangrove extends along the northern Gulf of Mexico as scattered shrubs.

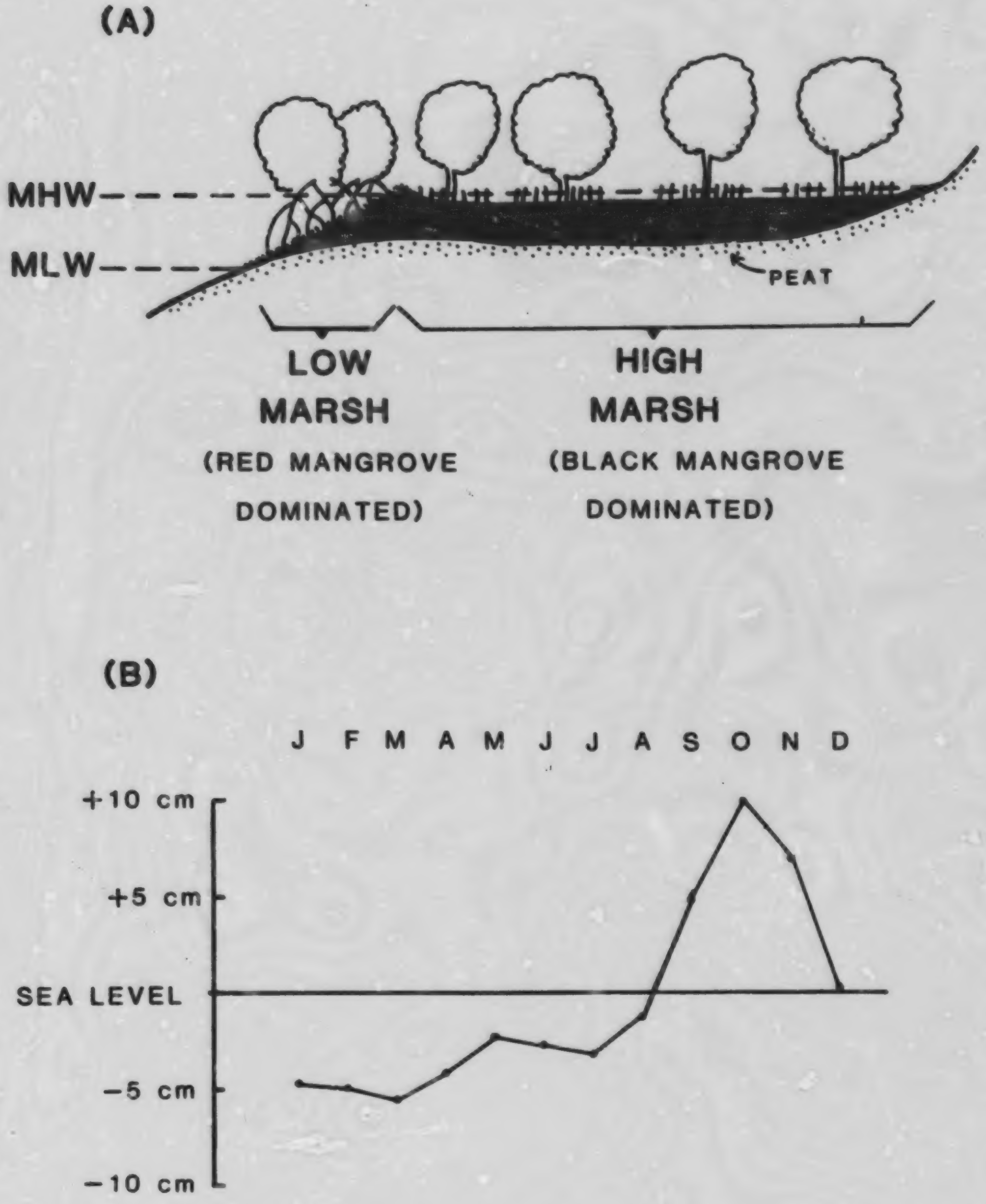

(A)
MHW
MLW
PEAT
LOW MARSH
(RED MANGROVE DOMINATED)
HIGH MARSH
(BLACK MANGROVE DOMINATED)
(B)
J F M A M J J A S O N D
+10 cm
+5 cm
SEA LEVEL
−5 cm
−10 cm

Figure 2. (a) A typical intertidal profile from south Florida showing the distribution of red and black mangrove (adapted from Provost 1974). (b) The pattern of annual sea level change in south Florida (Miami)(adapted from Provost 1974).

zonation). Furthermore, it is important to recognize that the intertidal zone in most parts of Florida changes seasonally (Provost 1974); there is a tendency for sea level to be higher in the fall than in the spring (Figure 2b). As a result the "high marsh" may remain totally dry during the spring and be continually submerged in the autumn. This phenomenon further complicates the textbook concept of the intertidal, "low marsh" red mangrove and the infrequently flooded, "high marsh" black mangrove.

Mangrove Acreage in Florida

Estimates of the total acreage occupied by mangrove communities in Florida vary widely between 430,000 acres and over 500,000 acres (174,000 ha to over 202,000 ha). Eric Heald (Tropical Bioindustries, 9869 Fern St., Miami, Fla.; personal communication 1981) has identified several reasons for the lack of agreement between estimates. These include: (1) inclusion or exclusion in surveys of small bays, ponds and creeks which occur within mangrove forests, (2) incorrect identification of mangrove areas from aerial photography as a result of inadequate "ground-truth" observations, poorly controlled aerial photography, and simple errors of planimetry caused by photography of inadequate scale.

The two most detailed estimates of area covered by mangroves in Florida are provided by the Coastal Coordinating Council, State of Florida (1974) and Birnhak and Crowder (1974). Considerable differences exist between the two estimates. The estimate of Birnhak and Crowder (1974), which is limited to certain areas of south Florida, appears to be unrealistically high, particularly for Monroe County (Eric Heald, personal communication 1981). Coastal Coordinating Council (1974) estimates a total of 469,000 acres (190,000 ha) within the State and suggests an expected margin of error of 15% (i.e. their estimate lies between 400,000 and 540,000 acres or 162,000 and 219,000 ha). According to this survey, ninety percent of Florida's mangroves are located in the four southern counties of Lee (35,000 acres or 14,000 ha), Collier (72,000 acres or 29,000 ha), Monroe (234,000 acres or 95,000 ha), and Dade (81,000 acres or 33,000 ha).

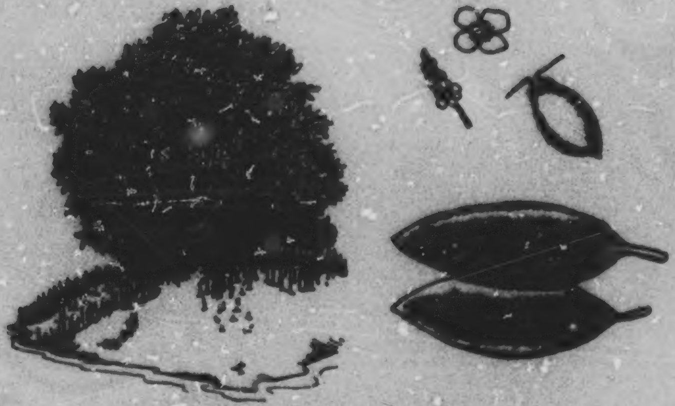
Much of the area covered by mangroves in Florida is presently owned by Federal, State or County governments, or by non-profit organizations such as the National Audubon Society. Approximately 280,000 acres (113,000 ha) fall into this category (Eric Heald, personal communication 1981). Most of this acreage is held by the Federal Government as a result of the land being including within the Everglades National Park.

1.4 MANGROVE SPECIES DESCRIPTIONS

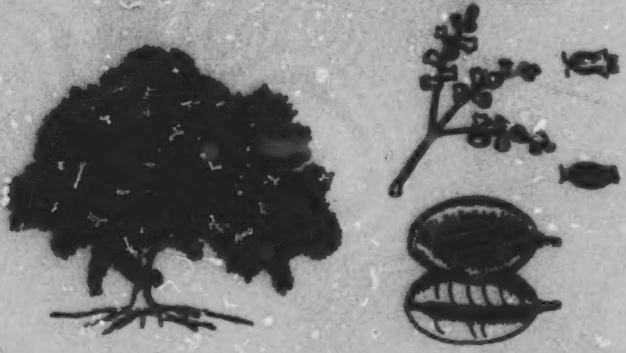
The following descriptions come largely from Carlton (1975) and Savage (1972); see these publications for further comments and photographs. For more detailed descriptions of germinating seeds (propagules) see section 2.3. The three species are shown in Figure 3.

The Black Mangrove (*Avicennia germinans*)

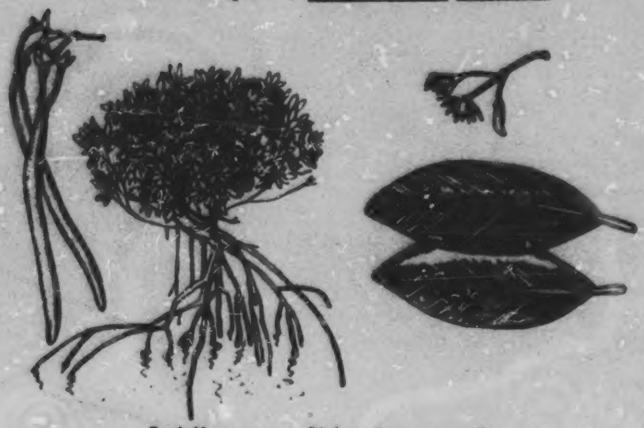
Avicennia germinans is synonymous with *A. nitida* and is a member of the family Avicenniaceae (formerly classed under Verbenaceae). The tree may reach a height of 20 m (64 ft) and has dark, scaly bark. Leaves are 5 to 10 cm (2 to 4 inches) in length, narrowly elliptic or oblong, shiny green above and covered with short, dense hairs below. The leaves are frequently encrusted with salt. This tree is characterized by long horizontal or "cable" roots with short vertical aerating branches (pneumatophores) that profusely penetrate the substrate below the tree. Propagules are lima-bean shaped, dark green while on the tree, and several centimeters (1 inch) long. The tree flowers in spring and early summer.



Black Mangrove, *Avicennia germinans*



White Mangrove, *Laguncularia racemosa*



Red Mangrove, *Rhizophora mangle*

Figure 3. Three species of Florida mangroves with propagules, flowers, and leaves.

The White Mangrove (Laguncularia racemosa)

The white mangrove is one of 450 species of plants in 18 genera of the family Combretaceae (synonymous with Terminaliaceae). It is a tree or shrub reaching 15 m (49 ft) or more in height with broad, flattened oval leaves up to 7 cm (3 inches) long and rounded at both ends. There are two salt glands at the apex of the petiole. The propagule is very small (1.0 to 1.5 cm or 0.4 to 0.6 inches long) and broadest at its apex. Flowering occurs in spring and early summer.

The Red Mangrove (Rhizophora mangle)

The red mangrove is one of more than 70 species in 17 genera in the family Rhizophoraceae. This tree may reach 25 m (80 ft) in height, has thin grey bark and dark red wood. Leaves may be 2 to 12 cm (1 to 5 inches) long, broad and blunt-pointed at the apex. The leaves are shiny, deep green above and paler below. It is easily identified by its characteristic "prop roots" arising from the trunk and branches. The pencil-shaped propagules are as much as 25 to 30 cm (10 to 12 inches) long after germination. It may flower throughout the year, but in Florida flowering occurs predominately in the spring and early summer.

1.5 MANGROVE COMMUNITY TYPES

Mangrove forest communities exhibit tremendous variation in form. For example, a mixed scrub forest of black and red mangroves at Turkey Point on Biscayne Bay bears little resemblance to the luxuriant forests, dominated by the same two species, along the lower Shark River.

Lugo and Snedaker (1974) provided a convenient classification system based on mangrove forest physiogomy. They identified six major community types resulting from different geological and hydrological processes. Each type has its own characteristic set of environmental variables such as soil type and depth, soil salinity range, and flushing rates. Each community type has characteristic ranges of primary production, litter decomposition and carbon export along with differences in nutrient recycling rates, and community components. The community types as shown in Figure 4 are as follows:

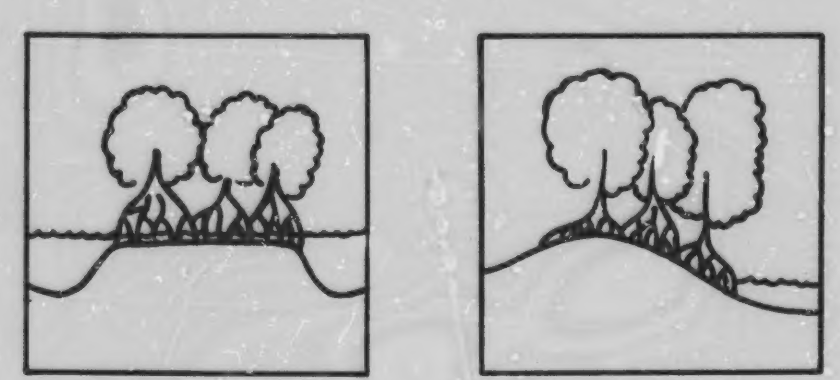
(1) Overwash mangrove forests - these islands are frequently overwashed by tides and thus have high rates of organic export. All species of mangroves may be present, but red mangroves usually dominate. Maximum height of the mangroves is about 7 m (23 ft).

(2) Fringe mangrove forests - mangroves form a relatively thin fringe along waterways. Zonation is typically as described by Davis (1940) (see discussion in section 3.2). These forests are best defined along shorelines whose elevations are higher than mean high tide. Maximum height of the mangroves is about 10 m (32 ft).

(3) Riverine mangrove forests - this community type includes the tall flood plain forests along flowing waters such as tidal rivers and creeks. Although a shallow berm often exists along the creek bank, the entire forest is usually flushed by daily tides. All three species of mangroves are present, but red mangroves (with noticeably few, short prop roots) predominate. Mangroves may reach heights of 18 to 20 m (60 to 65 ft).

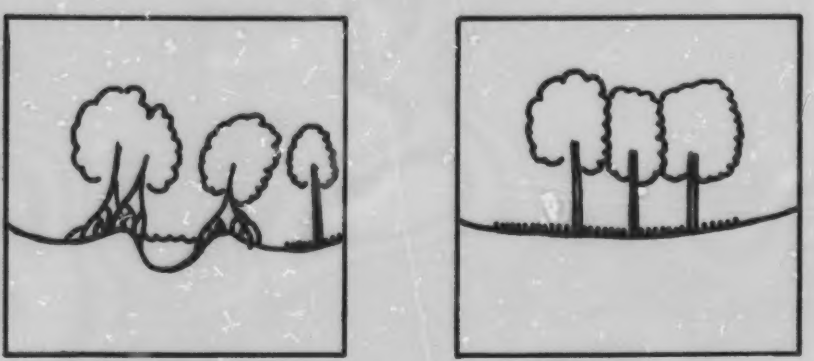
(4) Basin mangrove forests - these forests occur inland in depressions channeling terrestrial runoff toward the coast. Close to the coast they are influenced by daily tides and are usually dominated by red mangroves. Moving inland, the tidal influence lessens and dominance shifts to black and white mangroves. Trees may reach 15 m (49 ft) in height.

(5) Hammock forests - hammock mangrove communities are similar to the basin type except that they occur on ground that is slightly elevated (5 to 10 cm or 2 to 4 inches) relative to surrounding areas.



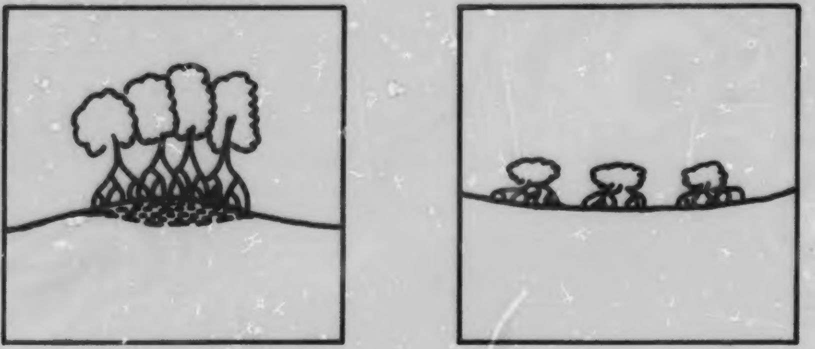
(1) OVERWASH FOREST

(2) FRINGE FOREST



(3) RIVERINE FOREST

(4) BASIN FOREST



(5) HAMMOCK FOREST

(6) SCRUB FOREST

Figure 4. The six mangrove community types (Lugo and Snedaker 1974).

All species of mangroves may be present. Trees rarely exceed 5 m (16 ft) in height.

(6) Scrub or dwarf forests - this community type is limited to the flat coastal fringe of south Florida and the Florida Keys. All three species are present. Individual plants rarely exceed 1.5 m (4.9 ft) in height, except where they grow over depressions filled with mangrove peat. Many of these tiny trees are 40 or more years of age. Nutrients appear to be limiting although substrate (usually limestone marl) must play a role.

Throughout this publication we have attempted to refer to Lugo and Snedaker's classification scheme wherever possible. Without a system of this type, comparisons between sites become virtually meaningless.

1.6 SUBSTRATES

Understanding mangrove-substrate relationships is complicated by the ability of mangroves to grow on many types of substrates and because they often alter the substrate through peat formation and by altering patterns of sedimentation. As a result, mangroves are found on a wide variety of substrates including fine, inorganic muds, muds with a high organic content, peat, sand, and even rock and dead coral if there are sufficient crevices for root attachment. Mangrove ecosystems, however, appear to flourish only on muds and fine-grained sands.

In Florida, the primary mangrove soils are either calcareous marl muds or calcareous sands in the southern part of the State and siliceous sands farther north (Kuenzler 1974). Sediment distribution and, hence, mangrove development, is controlled to a considerable extent by wave and current energy. Low energy shorelines accumulate fine-grained sediments such as mud and silt and usually have the best mangrove growth. Higher energy shorelines (more wave action or higher current velocities) are characterized by sandy sediments and less productive mangroves. If the wave energy becomes too great, mangroves will not be present. Of the three species of Florida mangroves, white mangroves appear to tolerate sandy substrates the best (personal observation), possibly because this species may tolerate a greater depth to the water table than the other two species.

Mangroves in Florida often modify the underlying substrate through peat deposition. It is not unusual to find layers of mangrove peat several meters thick underlying well-established mangrove ecosystems such as those along the southwest coast of Florida. Cohen and Spackman (1974) presented a detailed account of peat formation within the various mangrove zones of south Florida and also in areas dominated by black needle rush (Juncus roemerianus), smooth cordgrass (Spartina alterniflora) and a variety of other macrophytes; Cohen and Spackman (1974) also provide descriptions and photography to aid in the identification of unknown peat samples.

The following descriptions come from Cohen and Spackman (1974) and from the personal observations of W.E. Odum and E.J. Heald. Red mangroves produce the most easily recognized peat. More recent deposits are spongy, fibrous and composed to a great extent of fine rootlets (0.2 to 3.0 mm in diameter). Also present are larger pieces of roots (3 to 25 mm), bits of wood and leaves, and inorganic materials such as pyrite, carbonate minerals, and quartz. Older deposits are less easily differentiated although they remain somewhat fibrous. Peat which has recently been excavated is reddish-brown although this changes to brown-black after a short exposure to air. Older deposits are mottled reddish-brown; deposits with a high content of carbonates are greyish-brown upon excavation.

Cohen and Spackman (1974) were unable to find deposits of pure black mangrove or white mangrove peat suggesting that these two species may not form extensive deposits of peat while growing in pure stands. There are, however, many examples of peats which are mixtures of red mangrove material and black mangrove roots. They suggested that the black mangrove peats identified by Davis (1946) were probably mixtures of peat from several sources.

Throughout south Florida the substrate underlying mangrove forests may consist of complicated patterns of calcareous muds, marls, shell, and sand interspersed and overlain by layers of mangrove peat and with limestone bedrock at the bottom. Detailed descriptions of this complex matrix and its spatial variation were given by Davis (1940, 1943, 1946), Egler (1952), Craighead (1964), Zieman (1972) and Cohen and Spackman (1974) among others. Scoffin (1970) discussed the ability of red mangrove to trap and hold sediments about its prop roots. So called "land-building" by mangroves is discussed in section 3.2.

The long-term effect of mangrove peat on mangrove distribution is not entirely clear. Certainly, if there is no change in sea level or if erosion is limited, the accumulation of peat under stands of red mangroves combined with deposition and accumulation of suspended sediments will raise the forest floor sufficiently to lead to domination by black or white mangroves and, ultimately, more terrestrial species. Whether this is a common sequence of events in contemporary south Florida is not clear. It is clear that peat formtion is a passive process and occurs primarily where and when physical processes such as erosion and sea level rise are of minimal importance (Wanless 1974).

Zieman (1972) presented an interesting argument suggesting that mangrove peat may be capable of dissolving underlying limestone rock, since carbonates may dissolve at pH 7.8. Through this process, shallow depressions might become deeper and the overlying peat layer thicker without raising the surface of the forest floor.

Data on chemical characteristics of Florida mangrove soils and peat are limited. Most investigators have found mangrove substrates to be almost totally anaerobic. Lee (1969) recorded typical Eh values of -100 to -400 mv in mangrove peats. Such evidence of strongly reducing conditions are not surprising considering the fine-grained, high organic nature of most mangrove sediments. Although mangroves occur in low organic sediments (less than 1% organic matter), typical values for mangrove sediments are 10% to 20% organic matter.

Lee (1969) analyzed 3,000- to 3,500-year-old mangrove peat layers underlying Little Black Water Sound in Florida Bay for lipid carbon content. Peat lipid content varied between 0.6 and 2.7 mg lipid-C/gram of peat (dry wt) or about 3% of the total organic carbon total. These values usually increased with depth. Long chain fatty acids (C-16 and C-18) were the dominant fatty acids found.

Florida mangrove peats are usually acidic, although the presence of carbonate materials can raise the pH above 7.0. Zieman (1972) found red mangrove peats to range from pH 4.9 to 6.8; the most acid conditions were usually found in the center of the peat layer. Lee (1969) recorded a pH range from 5.8 to 6.8 in red mangrove peat at the bottom of a shallow embayment. Although Davis (1940) found a difference between red mangrove peat (5.0 to 5.5) and black mangrove peat (6.9 to 7.2), this observation has not been confirmed because of the previously mentioned difficulty in finding pure black mangrove peat.

Presumably, the acidic character of mangrove peat results from release of organic acids during anaerobic decomposition and from the oxidation of reduced sulfur compounds if the peat is dried in the presence of oxygen. This last point explains why "reclaimed" mangrove areas often develop highly acidic soils (pH 3.5 to 5.0) shortly after reclamation. This "cat clay" problem has greatly complicated the conversion of mangrove regions to agricultural land in Africa and southeast Asia (Hesse 1961; Hart 1962, 1963; Macnae 1968).

In summary, although current understanding of mangrove peats and soils is fragmentary and often contradictory, we can outline several generalizations:

(1) Mangroves can grow on a wide variety of substrates including mud, sand, rock, and peat.

(2) Mangrove ecosystems appear to flourish on fine-grained sediments which are usually anaerobic and may have a high organic content.

(3) Mangrove ecosystems which persist for some time may modify the underlying substrate through peat formation. This appears to occur only in the absence of strong physical forces.

(4) Mangrove peat is formed primarily by red mangroves and consists predominantly of root material.

(5) Red mangrove peats may reach thicknesses of several meters, have a relatively low pH, and may be capable of dissolving underlying layers of limestone.

(6) When drained, dried, and aerated, mangrove soils usually experience dramatic increases in acidity due to the oxidation of reduced sulfur compounds. This greatly complicates their conversion to agriculture.

1.7 WATER QUALITY

Water quality characteristics of surface waters flowing through Florida mangrove ecosystems exhibit great variation from one location to the next. Proximity to terrestrial ecosystems, the ocean, and human activities are all important in determining overall water quality. Equally important is the extent of the mangrove ecosystem since drastic alterations in water quality can occur within a stand of mangroves.

In general, the surface waters associated with mangroves are characterized by (1) a wide range of salinities from virtually fresh water to above 40 ppt (discussed in section 2.2), (2) low macronutrient concentrations (particularly phosphorous), (3) relatively low dissolved oxygen concentrations, and (4) frequently increased water color and turbidity. The last three characteristics are most pronounced in extensive mangrove ecosystems such as those adjacent to the Everglades and least pronounced in small, scattered forests such as the overwash islands in the Florida Keys.

Walsh (1967), working in a mangrove swamp in Hawaii, was one of the first to document the tendency of mangrove ecosystems to act as a consumer of oxygen and a sink for nutrients such as nitrogen and phosphorous. Carter et al. (1973) and Lugo et al. (1976) confirmed these observations for Florida mangrove swamps. Evidently, nutrients are removed and oxygen consumed by a combination of periphyton on mangrove prop roots, mud, organic detritus on the sediment surface, the fine root system of the mangroves, small invertebrates, benthic and epiphytic algae, and bacteria and fungi on all these surfaces.

The results of oxygen depletion and nutrient removal are (1) dissolved oxygen concentrations below saturation, typically 2 to 4 ppm and often near zero in stagnant locations and after heavy, storm-generated runoff, (2) very low total phosphorus values, frequently below detection limits, and (3) moderate total nitrogen values (0.5 to 1.5 mg/l). In addition, TOC (total organic carbon) may range from 4 to 50 ppm or even higher after rain; Eric Heald (personal communication 1981) has measured DOC (dissolved organic carbon) values as high as 110 ppm in water flowing from mangroves to adjacent bays. Turbidity usually falls in the 1 to 15 JTU (Jackson turbity units) range. The pH of the water column in Florida swamps is usually between 6.5 and 8.0 and alkalinity between 100 to 300 mg/l. Obviously, exceptions to all of these trends can occur. Both natural and human disturbance can raise macronutrient levels markedly.

CHAPTER 2. AUTECOLOGY OF MANGROVES

2.1 ADAPTATIONS TO NATURAL STRESS - ANAEROBIC SEDIMENTS

Mangroves have a series of remarkable adaptations which enable them to flourish in an environment characterized by high temperatures, widely fluctuating salinities, and shifting, anaerobic substrates. In this section we review a few of the most important adaptations.

The root system of mangroves provides the key to existence upon unfriendly substrates (see Gill and Tomlinson 1971 for an anatomical review of mangrove roots). Unlike most higher plants, mangroves usually have highly developed aerial roots and modest below-ground root systems. The aerial roots allow atmospheric gases to reach the underground roots which are embedded in anaerobic soils. The red mangrove has a system of stilt or prop roots which extend a meter (3 ft) or more above the surface of the soil and contain many small pores (lenticels) which at low tide allow oxygen to diffuse into the plant and down to the underground roots by means of open passages called aerenchyma (Scholander et al. 1955). The lenticels are highly hydrophobic and prevent water penetration into the aerenchyma system during high tide (Waisel 1972).

The black mangrove does not have prop roots, but does have small air roots or pneumatophores which extend vertically upward from the underground roots to a height of 20 to 30 cm (8 to 12 inches) above the soil. These pneumatophores resemble hundreds of tiny fingers sticking up out of the mud underneath the tree canopy. At low tide, air travels through the pneumatophores into the aerenchyma system and then to all living root tissues. The white mangrove usually does not have either prop roots or pneumatophores, but utilizes lenticels in the lower trunk to obtain oxygen for the aerenchyma system. "Peg roots" and pneumatophores may be present in certain situations (Jenik 1967).

Mangroves achieve structural stability in at least two ways. Species such as the red mangrove use the system of prop roots to provide a more or less firm foundation for the tree. Even though the prop roots are anchored with only a modest assemblage of underground roots, the horizontal extent of the prop root system insures considerable protection from all but the worst of hurricanes. Other mangrove species, including the black mangrove, obtain stability with an extensive system of shallow, underground "cable" roots that radiate out from the central trunk for a considerable distance in all directions; the pneumatophores extend upward from these cable roots. As in all Florida mangroves, the underground root system is shallow and a tap root is lacking (Walsh 1974). As Zieman (1972) found, individual roots, particularly of red mangroves, may extend a meter or more downward in suitable soils.

From the standpoint of effectiveness in transporting oxygen to the underground roots, both prop roots and cable roots seem equally effective. From the perspective of stability, the prop roots of red mangroves appear to offer a distinct advantage where wave and current energies are high.

Unfortunately, as pointed out by Odum and Johannes (1975), the same structure which allows mangroves to thrive in anaerobic soil is also one of the tree's most vulnerable components. Exposed portions of the aerial root system are susceptible to clogging by fine suspended material, attack by root borers, and prolonged flooding (discussed further in section 12.1). Such extended stress on the aerial roots can kill the entire tree.

2.2 ADAPTATIONS TO NATURAL STRESS - SALINITY

Mangroves accommodate fluctuations and extremes of water and soil salinity through a variety of mechanisms, although not all mechanisms are necessarily present in the same species. Scholander et al. (1962) reported experimental evidence for two major methods of internal ion regulation which they identified in two different groups of mangroves: (1) the salt exclusion species and (2) the salt excretion species. In addition, some mangroves utilize succulence and the discarding of salt-laden organs or parts (Teas 1979).

The salt-excluding species, which include the red mangrove, separate freshwater from sea water at the root surface by means of a non-metabolic ultrafiltration system (Scholander 1968). This "reverse osmosis" process is powered by a high negative pressure in the xylem which results from transpiration at the leaf surface. Salt concentration in the sap of salt-excluding mangroves is about 1/70 the salt concentration in sea water, although this concentration is almost 10 times higher than found in normal plants (Scholander et al. 1962).

Salt-secreting species, including black and white mangroves (Scholander 1968), use salt glands on the leaf surface to excrete excess salt. This is probably an enzymatic process rather than a physical process since it is markedly temperature sensitive (Atkinson et al. 1967). The process appears to involve active transport with a requirement for biochemical energy input. As a group, the salt secreters tend to have sap salt concentrations approximately 10 times higher (1/7 the concentration of sea water) than that of the salt excluders.

In spite of these two general tendencies, it is probably safe to say that individual species utilize a variety of mechanisms to maintain suitable salt balance (Albert 1975). For example, the red mangrove is an effective, but not perfect, salt excluder. As a result this species must store and ultimately dispose of excess salt in leaves and fruit (Teas 1979). Most salt secreters, including white and black mangroves, are capable of limited salt exclusion at the root surface. The white mangrove, when exposed to hypersaline conditions, not only excludes some salt and secretes excess salt through its salt glands, but also develops thickened succulent leaves and discards salt during leaf fall of senescent leaves (Teas 1979).

There appears to be some variation in the salinity tolerance of Florida mangroves. The red mangrove is probably limited by soil salinities above 60 to 65 ppt. Teas (1979) recalculated Bowman's (1917) data and concluded that transpiration in red mangrove seedlings ceases above 65 ppt. Cintron et al. (1978) found more dead than living red mangrove trees where interstitial soil salinities exceeded 65 ppt.

On the other hand, white and black mangroves, which both possess salt excretion and limited salt exclusion mechanisms, can exist under more hypersaline conditions. Macnae (1968) reported that black mangroves can grow at soil salinities greater than 90 ppt. Teas (1979) reported dwarfed and gnarled black and white mangroves occurring in Florida at soil salinities of 80 ppt.

There may be an additional factor or factors involved in salinity tolerance of mangroves. McMillan (1975) found that seedlings of black and white mangroves survived short-term exposures to 80 ppt and 150 ppt sea water if they were grown in a soil with a moderate clay content. They failed to survive these salinities, however, if they were grown in sand. A soil with 7% to 10% clay appeared to be adequate for increased protection from hypersaline conditions.

Vegetation-free hypersaline lagoons or bare sand flats in the center of mangrove ecosystems have been described by many authors (e.g., Davis 1940; Fosberg 1961; Bacon 1970). These features have been variously called salitrals (Holdridge 1940), salinas, salterns, salt flats, and salt barrens. Evidently, a combination of low seasonal rainfall, occasional inundation by sea water, and high evaporation rates results in soil salinities above 100 ppt, water temperatures as high as 45°C (113°F) in any shallow, standing water, and subsequent mangrove death (Teas 1979). Once established, salinas tend to persist unless regular tidal flushing is enhanced by natural or artificial changes in tidal circulation.

Although salinas occur frequently in Florida, they are rarely extensive in area. For example, between Rookery Bay and Marco Island (south of Naples, Florida) there are a series of salinas in the black mangrove-dominated zone on the upland side of the mangrove swamps. These hypersaline lagoons occur where the normal flow of fresh water from upland sources has been diverted, presumably resulting in elevated soil salinities during the dry winter months.

In summary, salinity is a problem for mangroves only under extreme hypersaline conditions. These conditions occur naturally in Florida in irregularly flooded areas of the "high swamp" above the normal high tide mark and are accompanied by high soil salinities. Florida mangroves, listed in order of increasing salinity tolerance, appear to be red, white, and black.

2.3 REPRODUCTIVE STRATEGIES

As pointed out by Rabinowitz (1978a), virtually all mangroves share two common reproductive strategies: dispersal by means of water (van der Pijl 1972) and vivipary (Macnae 1968; Gill and Tomlinson 1969). Vivipary means that the embryo develops continuously while attached to the parent tree and during dispersal. Since there is uninterrupted development from zygote through the embryo to seedling without any intermediate resting stages, the word "seed" is inappropriate for viviparous species such as mangroves; the term "propagule" is generally used in its place.

While the phenology of black and white mangroves remains sketchy, Gill and Tomlinson (1971) thoroughly described the sequence of flowering in the red mangrove. Flowering in this species may take place at any time of the year, at least in extreme south Florida, but reaches a maximum in the late spring and summer. The flowers open approximately 1 to 2 months after the appearance of buds. The flower remains intact only 1 to 2 days; this probably accounts for the low fertilization rate, estimated by Gill and Tomlinson at 0% to 7.2%. Propagule development is slow, ranging from 8 to 13 months. Savage (1972) mentions that on the Florida gulf coast, red mangrove propagules mature and fall from the tree from July to September. Within the Everglades National Park, black mangroves flower from May until July and bear fruit from August until November while white mangroves flower from May to August and bear fruit from July to October (Loope 1980).

The propagules of the three species of Florida mangroves are easy to differentiate. The following descriptions all come from Rabinowitz (1978a). White mangrove propagules are small and flattened, weigh less than a gram, are about 2 cm long, are pea-green when they fall from the parent tree, and turn mud-brown in two days or so. The pericarp (wall of the ripened propagule) serves as a float and is not shed until the seedling is established. During dispersal the radicle (embryonic root) emerges from the propagule. This germination during dispersal has led Savage (1972) to refer to the white mangrove as "semi-viviparous".

The propagules of the black mangrove when dropped from the tree are oblong-elliptical (resemble a flattened olive), weigh about 1 g and are about 2 cm long. The pericarp is lost within a few days after dropping from the tree; at this point the cotyledons (primary leaves) unfold and the propagule resembles two butterflies on top of one another.

Propagules of the red mangrove undergo extensive vivipary while on the tree. When propagules fall from the tree they resemble large green beans. They are rod-shaped with pointed ends, about 20 cm long, and weigh an average of 15 g.

Propagules of all three species float and remain viable for extended periods of time. Apparently, there is an obligate dispersal time for all Florida mangroves, i.e., a certain period of time must elapse during dispersal for germination to be complete and after which seedling establishment can take place. Rabinowitz (1978a) estimates the obligate dispersal period at approximately 8 days for white mangroves, 14 days for black, and 40 days for red. She further estimates the additional time for root establishment at 5, 7, and 15 days for white, black, and red mangroves, respectively. Her estimate for viable longevity of the propagules is 35 days for white mangroves and 110 days for black. Davis (1940) reports viable propagules of red mangroves that had been kept floating for 12 months.

Rabinowitz (1978a) also concluded that black and white mangroves require a stranding period of 5 days or more above the influence of tides to take hold in the soil. As a result, these two species are usually restricted to the higher portions of the mangrove ecosystem where tidal effects are infrequent.

The elongated red mangrove propagule, however, has the potential to become established in shallow water with tidal influence. This happens in at least two ways: (1) stranding in a vertical position (they float vertically) or (2) stranding in a horizontal position, rooting and then vertical erection by the plant itself. Lawrence (1949) and Rabinowitz (1978a) felt that the latter was the more common method. M. Walterding (Calif. Acad. Sci., San Francisco; personal communication 1980) favors vertical establishment; based upon his observations, surface water turbulence works the propagule into the substrate during falling tides.

Mortality of established seedlings seems to be related to propagule size. Working in Panama, Rabinowitz (1978b) found that the mortality rate of mangrove seedlings was inversely correlated with initial propagule size. The white mangrove, which has the smallest propagule, has the highest rate of seedling mortality. The black mangrove has an intermediate mortality rate while the red mangrove, with the largest propagule, has the lowest seedling mortality rate. She concluded that species with small propagules establish new cohorts annually but die rapidly, while species such as the red mangroves may have long-lived and often overlapping cohorts.

Propagule size and seedling mortality rates are particularly important in considerations of succession and replacement in established mangrove forests. Light is usually the most serious limiting factor underneath existing mangrove canopies. Rabinowitz (1978b) suggested that species with short-lived propagules must become established in an area which already has adequate light levels either due to tree fall or some other factor. In contrast, red mangrove seedlings can become established under an existing, dense canopy and then, due to their superior embryonic reserves, are able to wait for months for tree fall to open up the canopy and present an opportunity for growth.

2.4 BIOMASS PARTITIONING

Few investigators have partitioned the total biomass, aboveground and belowground, contained in a mangrove tree. An analysis of red mangroves in a Puerto Rican forest by Golley et al. (1962) gives some insight into what might be expected in south Florida. Aboveground and belowground biomass existed in a ratio of 1:1 if fine roots and peat are ignored (Figure 5). In this case, peat and very fine roots (smaller than 0.5 cm diameter) exceeded remaining biomass by 5:1. Lugo et al. (1976) reported the following values for a south Florida red mangrove overwash forest. All values were reported in dry grams per square meter, plus and minus one standard error, and ignoring belowground biomass. They found 710 ± 22 g/m^2 of leaves, 12.8 ± 15.3 g/m^2 of propagules, 7043 ± 7 g/m^2 of wood, 4695 ± 711 g/m^2 of prop roots and 1565 ± 234.5 g/m^2 of detritus on the forest floor.

Biomass partitioning between different species and locations must be highly variable. The age of the forest will influence the amount of wood biomass;

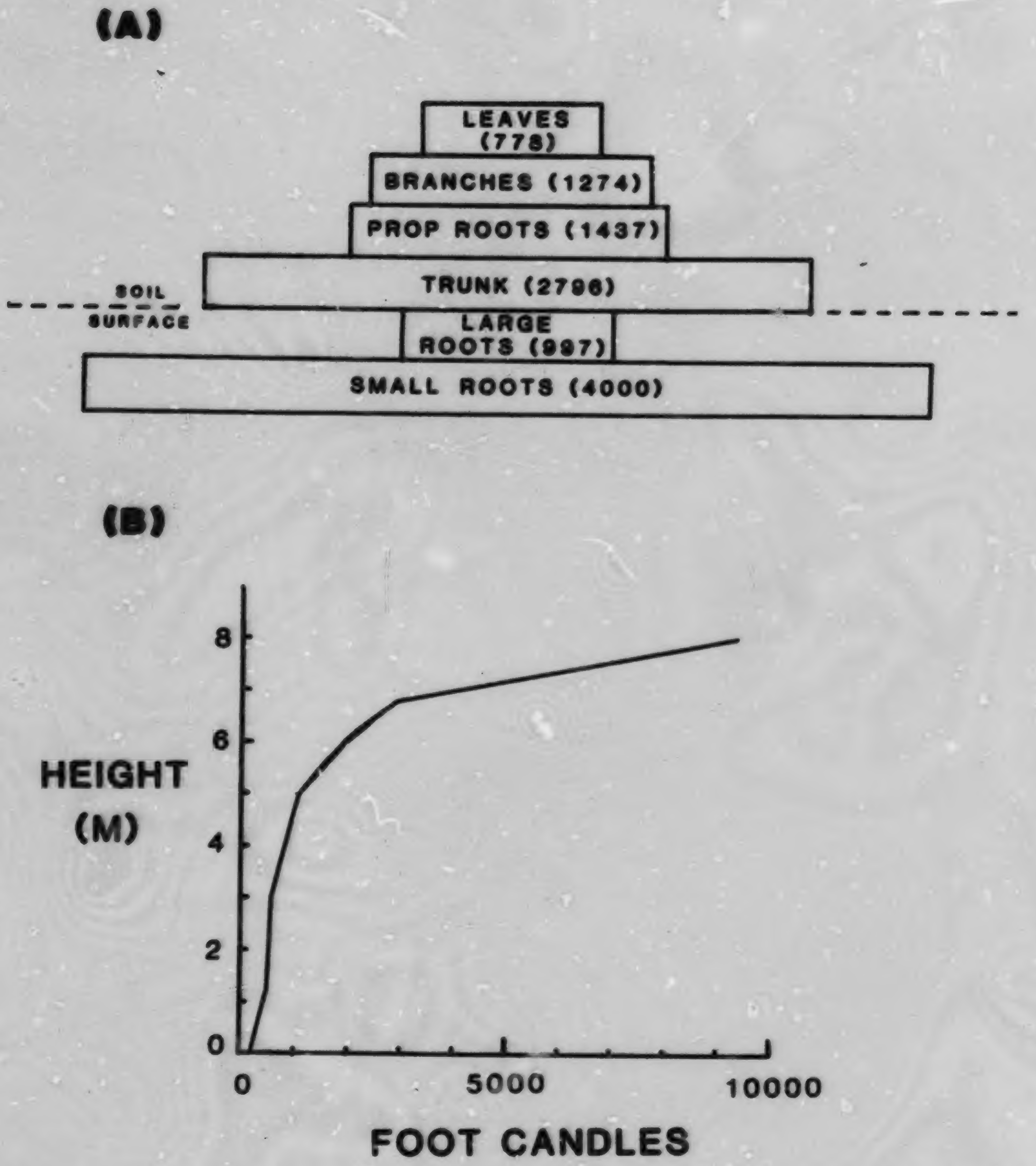


Figure 5. (a) Aboveground and belowground biomass of a Puerto Rican red mangrove forest. Values in parentheses are dry g/m^2; large roots = 2 cm+ in diameter, small roots = 0.5 - 1.0 cm. (b) Vertical distribution of light intensity in the same forest; canopy height is 8 m (26 ft) (both figures adapted from Golley et al. 1962).

detritus varies enormously from one site to the next depending upon the amount of fluvial transport. The biomass characteristics of a scrub forest probably bear little resemblance to those of a fringing forest. At the present time, there is not enough of this type of data available to draw many conclusions. One intriguing point is that red mangrove leaf biomass averages between 700 and 800 g/m^2 at various sites with very different forest morphologies (Odum and Heald 1975a). This may be related to the tendency of mangrove canopies, once they have become established, to inhibit leaf production at lower levels through self-shading.

Golley et al. (1962) showed that the red mangrove canopy is an extremely efficient light interceptor. Ninety-five percent of the available light had been intercepted 4 m (13 ft) below the top of the canopy (Figure 5). As a result, 90% of the leaf biomass existed in the upper 4 m of the canopy. Chlorophyll followed the same pattern of distribution.

The leaf area index (LAI) of mangrove forests tends to be relatively low. Golley et al. (1962) found a LAI of 4.4 for a Puerto Rican red mangrove forest. Lugo et al. (1975) reported a LAI of 5.1 for a Florida black mangrove forest and 3.5 for a Florida fringe red mangrove forest. A different black mangrove forest, in Florida, was found to have values ranging from 1 to 4 and an average of 2 to 2.5 (Lugo and Zucca 1977). These values compare with LAI's of 10 to 20 recorded for most tropical forests (Golley et al. 1974). The low leaf area values of mangrove forests can be attributed to at least three factors: (1) effective light interception by the mangrove canopy, (2) the inability of the lower mangrove leaves to flourish at low light intensities, and (3) the absence of a low-light-adapted plant layer on the forest floor.

2.5 PRIMARY PRODUCTION

Prior to 1970 virtually no information existed concerning the productivity of mangroves in Florida. Since that time knowledge has accumulated rapidly, but it is still unrealistic to expect more than preliminary statements about Florida mangrove productivity. This deficiency can be traced to (1) the difficulties associated with measurements of mangrove productivity and (2) the variety of factors that affect productivity and the resulting variations that exist from site to site.

Productivity estimates come from three methods: (1) harvest, (2) gas exchange, and (3) litter fall. Harvest methods require extensive manpower and knowledge of the age of the forest. They are best employed in combination with silviculture practices. Since silviculture of south Florida mangroves is practically non-existent, this method has rarely been used in Florida Noakes (1955), Macnae (1968), and Wal (1974) should be consulted for productivity estimates based on this technique in other parts of the world.

Gas exchange methods, based on measurements of CO_2 changes, have the advantage of precision and response to short-term changes in light, temperature, and flooding. They include both aboveground and belowground production. On the negative side, the necessary equipment is expensive and tricky to operate properly. Moreover, extrapolations from short-term measurements to long-term estimates offer considerable opportunity for error. Nevertheless, the best estimates of productivity come from this method.

The litter fall technique (annual litter fall x 3 = annual net primary production) was proposed by Teas (1979) and is based on earlier papers by Bray and Gorham (1964) and Golley (1972) for other types of forests. This is a quick and dirty method although the lack of precision remains to be demonstrated for mangroves. An even quicker and dirtier method proposed by Teas (1979) is to (1) estimate leaf standing crop (using various techniques including harvesting or light transmission relationships) and (2) multiply by three. This assumes an annual leaf turnover of one, which is supported by the data of Heald (1969) and Pool et al. (1977).

Mangrove productivity is affected by many factors; some of these have been recognized and some remain totally obscure. Carter et al. (1973) propose lumping these factors into two broad categories: tidal and water chemistry. We believe that a number of additional categories should be considered.

A minimal, though incomplete, list of factors controlling mangrove productivity must include the following:

- species composition of the stand
- age of the stand
- presence or absence of competing species
- degree of herbivory
- presence or absence of disease and parasites
- depth of substrate
- substrate type
- nutrient content of substrate
- nutrient content of overlying water
- salinity of soil and overlying water
- transport efficiency of oxygen to root system
- amount of tidal flushing
- relative wave energy
- presence or absence of nesting birds
- periodicity of severe stress (hurricanes, fire, etc.)
- time since last severe stress
- characteristics of ground water
- inputs of toxic compounds or nutrients from human activities
- human influences such as diking, ditching, and altering patterns of runoff.

In spite of the difficulties with various methods and the interaction of controlling factors, it is possible to make general statements about certain aspects of mangrove productivity. For example, Waisel's (1972) statement that mangroves have low transpiration rates seems to be generally true in Florida. Lugo et al. (1975) reported transpiration rates of 2,500 g H_2O/m^2/day for mangrove leaves in a fringing red mangrove forest and 1,482 g H_2O/m^2/day for black mangrove leaves. This is approximately one-third to one-half the value found in temperate broad leaf forests on hot dry days, but comparable to tropical rainforests (H.T. Odum and Jordan 1970). The low transpiration rates of mangroves are probably related to the energetic costs of maintaining sap pressures of -35 to -60 atmospheres (Scholander et al. 1965).

Litter fall (leaves, twigs, bark, fruit, and flowers) of Florida mangrove forests appears to average 2 to 3 dry g/m^2day in most well-developed mangrove stands (see discussion in section 3.4). This can be an order of magnitude lower in scrub forests.

Wood production of mangroves appears to be high compared to other temperate and tropical trees, although no measurements from Florida are available. Noakes (1955) estimated that the wood production of an intensively managed Malayan forest was 39.7 metric tons/ha/year. Teas (1979) suggested a wood production estimate of 21 metric tons/ha/year for a mature unmanaged red mangrove forest in south Florida. His figure was calculated from a litter/total biomass relationship and is certainly subject to error.

Representative estimates of gross primary production (GPP) net primary production (NPP), and respiration (R) of Florida mangroves are given in Table 1a. Compared to net primary production (NPP) estimates from other ecosystems, including agricultural systems (E.P. Odum 1971), it appears that mangroves are among the world's most productive ecosystems. Healthy mangrove ecosystems appear to be more productive than sea grass, marsh grass and most other coastal systems.

Further examination of Table 1a reveals several possible tendencies. The first hypothetical tendency, as discussed by Lugo et al. (1975), is for red mangroves to have the highest total net production, black to have intermediate values and white the lowest. This conclusion assumes that the plants occur within the zone for which they are best adapted (see section 3.2 for discussion of zonation) and are not existing in an area with strong limiting factors. A scrub red mangrove forest, for example, growing under stressed conditions (high soil salinity or low nutrient supply), has relatively low net productivity (Teas 1979). The pre-eminent position of red mangroves is shown by the comparative measurements of photosynthesis in Table 1b; measurements were made within canopy leaves of trees growing within their zones of optimal growth.

A second noteworthy tendency is that red mangrove GPP decreases with increasing salinity while GPP of black and white mangroves increases with increasing salinity up to a point. Estimates of Hicks and Burns (1975) demonstrate that this may be a real tendency (Table 1c).

Data presented by Miller (1972), Carter et al. (1973), Lugo and Snedaker (1974), and Hicks and Burns (1975) suggest a third hypothetical tendency, assuming occurrence of the species within its adapted zone. It appears that the black mangrove typically has a much higher respiration rate, lower net productivity, and lower GPP/R ratio than the red mangrove. This can be attributed at least partially, to the greater salinity stress under which the black mangrove usually grows; this leads to more osmotic work.

These three apparent tendencies have led Carter et al. (1973) and Lugo et al. (1976) to propose a fourth tendency, an inverted U-shaped relationship between waterway position and net mangrove community productivity (Figure 6). This tendency is best understood by visualizing a typical gradient on the southwest coast of Florida. At the landward end of the gradient, salinities are very low, nutrient runoff from terrestrial ecosystems may be high and tidal amplitude is minor. At the seaward end, salinities are relatively high, tidal amplitude is relatively great and nutrient concentrations tend to be lower. At either end of the gradient, the energetic costs are high and a large percentage of GPP is used for self-maintenance; at the landward end, competition from freshwater plant species is high and at the seaward end, salinity stress may be limiting. In this scenario, the highest NPP occurs in the middle region of the gradient; salinity and tidal amplitude are high enough to limit competition while tidal flushing and moderate nutrient levels enhance productivity. Hicks and Burns (1975) present data to support this hypothesis.

In addition to these hypotheses generated from field data, there have been two significant, published attempts to derive hypotheses from mathematical simulation models of mangroves. The first (Miller 1972) is a model of primary production and transpiration of red mangrove canopies and is based upon equations which utilize field measurements of the energy budgets of individual leaves. This model predicts a variety of interesting trends which need to be further field tested. One interesting hypothesis generated by the model is that maximum photosynthesis of red mangrove stands should occur with a leaf area index (LAI) of 2.5 if no acclimation to shade within the canopy occurs; higher LAI's may lead to decreased production. Another prediction is that red mangrove production is most affected by air temperature and humidity and, to a lesser degree, by the amount of solar

Table 1a. Estimates of mangrove production in Florida. All values are gC/m^2/day except annual NPP = metric tons/ha/yr. GPP = gross primary production, NPP = net primary production, L.F. = annual litter fall X 3, R = red mangrove, W = white mangrove, B = black mangrove. Observations 6 and 7 were on sunny days, 8 and 9 on cloudy days.

Species	GPP	Respiration	NPP	Annual NPP	Method	Reference
Mixed R, W,B	24.0	11.4	12.6	46.0	Gas exchange	Hicks & Burns (1975)
B	18.0	12.4	5.6	20.5	Gas exchange	Lugo & Snedaker (1974)
Mature R	---[a]	---[a]	8.8	20.5	L.F.	Teas (1979)
Scrub R	---[a]	---[a]	1.0	3.8	L.F.	Teas (1979)
Basin B	---[a]	---[a]	2.4	8.6	L.F.	Teas (1979)
R (June)	12.8	7.3	5.5	20.3	Gas exchange	Miller (1972)
R (Jan.)	9.4	5.1	4.3	15.7	Gas exchange	Miller (1972)
R (June)	10.3	6.8	3.5	12.8	Gas exchange	Miller (1972)
R (Jan.)	10.2	5.0	5.2	18.8	Gas exchange	Miller (1972)
Mixed R,W, B(riverine)	13.9	9.1	4.8	17.5	Gas exchange	Carter et al. (1973)
Mixed R,W, B(basin)	11.8	4.3	7.5	27.4	Gas exchange	Carter et al. (1973)
B	9.0	6.2	2.8	9.4	Gas exchange	Lugo et al. (1976)
R	6.3	1.9	4.4	16.1	Gas exchange	Lugo et al. (1976)

[a] Method does not produce this data.

Table 1b. Comparative measurements of photosynthesis in $gC/m^2/day$ (Lugo et al. 1975).

Mangrove type	Daytime net photosynthesis	Nighttime respiration	P_n/R
Red	1.38	0.23	6.0
Black	1.24	0.53	2.3
White	0.58	0.17	3.4
Red (seedling)	0.31	1.89	negative

Table 1c. Gross primary production (GPP) at different salinities (Hicks and Burns 1975).

Mangrove type	Average surface salinity (ppt)	GPP ($gC/m^2/day$)
Red	7.8	8.0
Red	21.1	3.9
Red	26.6	1.6
Black	7.8	2.3
Black	21.1	5.7
Black	26.6	7.5
White	21.1	2.2
White	26.6	4.8

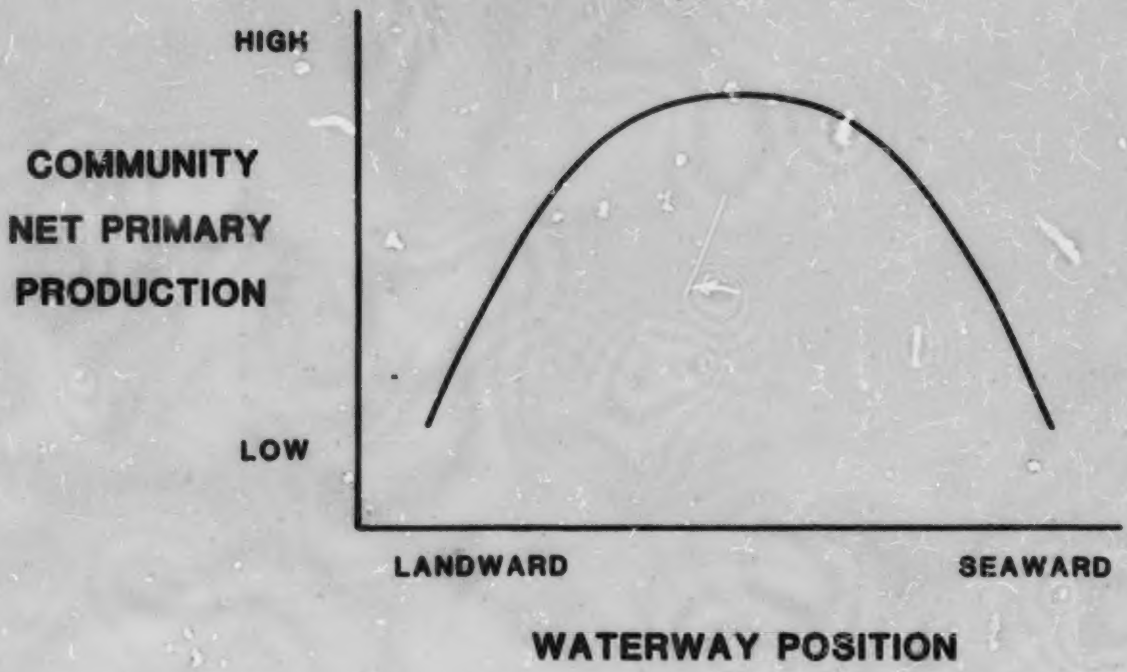


Figure 6. The hypothetical relationship between waterway position and community net primary production of Florida mangrove forests (based on Carter et al. 1973).

radiation within the ambient range. Gross photosynthesis per unit leaf area was greater at the top of the tree canopy than at the bottom, although the middle levels had the greatest production.

Miller (1972) concluded by suggesting that the canopy distribution of red mangrove leaves is nearly optimal for efficient water utilization rather than production. This indicates that the canopy is adapted to maximizing production under conditions of saturated water supply.

The mangrove ecosystem model reported by Lugo et al. (1976) provides hypotheses on succession, time to arrive at steady state conditions (see section 3.2), and several aspects of productivity. The model output suggests that the relative amount of tidal amplitude does not affect GPP significantly; instead, GPP appears to be extremely sensitive to inputs of terrestrial nutrients. It follows that locations with large amounts of nutrient input from terrestrial sources (riverine mangrove communities) have high rates of mangrove production (see section 3.3). All simulation model-generated hypotheses need to be field tested with a particularly critical eye, since the simplifying assumptions that are made in constructing the model can lead to overly simplistic answers.

Mangrove productivity research remains in an embryonic stage. Certain preliminary tendencies or hypotheses have been identified, but much work must be done before we can conclude that these hypotheses cannot be falsified.

2.6 HERBIVORY

Direct herbivory of mangrove leaves, leaf buds, and propagules is moderately low, but highly variable from one site to the next. Identified grazers of living plant parts (other than wood) include the white-tailed deer, *Odocoileus virginianus*, the mangrove tree crab, *Aratus pisonii*, and insects including beetles, larvae of lepidopterans (moths and butterflies), and orthopterans (grasshoppers and crickets).

Heald (1969) estimated a mean grazing effect on North River red mangrove leaves of 5.1% of the total leaf area; values from leaf to leaf were highly variable ranging from 0 to 18%. Beever et al. (1979) presented a detailed study of grazing by the mangrove tree crab. This arboreal grapsid crab feeds on numerous items including beetles, crickets, caterpillars, littoral algae, and dead animal matter. In Florida, red mangrove leaves form an important component of the diet. Beever et al. (1979) measured tree crab grazing ranging from 0.4% of the total leaf area for a Florida Keys overwash forest to 7.1% for a fringing forest at Pine Island, Lee County, Florida. The researchers also found that tree crab grazing rates are related to crab density. Low densities (one crab/m^3) resulted in low leaf area damage (less than 1% of total leaf area). High densities (four crabs/m^3) were accompanied by leaf area damage ranging from 4% to 6% (see section 6.2).

Onuf et al. (1977) investigated insect herbivory in fringing and overwash red mangrove forests in the Indian River estuary near Ft. Pierce, Florida. They found six major herbivorous insect species, five lepidopteran larvae and a beetle. Comparisons were made at a high nutrient site (input from a bird rookery) and a low nutrient site. Both red mangrove production and leaf nitrogen were significantly higher at the high nutrient site. This resulted in a four-fold greater loss to herbivores (26% of total leaf area lost to grazing); this increased grazing rate more than offset the increased leaf production due to nutrient input.

Calculations of leaf area damage may underestimate the impact of herbivores on mangroves. For example, the larvae of the olethreutid moth, *Ecdytolopha* sp., develops within red mangrove leaf buds and causes the loss of entire leaves. All stages of the beetle, *Poecilips* rhizophorae, attack mangrove propagules while still attached to the parent tree (Onuf et al. 1977).

2.7 WOOD BORERS

Many people have the mistaken idea that mangrove wood is highly resistant to marine borers. While this may be true to a limited extent for certain mangrove species in other parts of the world, none of the Florida mangroves have borer-resistant wood. Southwell and Boltman (1971) found that the wood of red, black, and white mangroves has no resistance to Teredo, Pholad and Simnorid borers; pieces of red mangrove wood were completely destroyed after immersion in ocean water for 14 months.

An interesting controversy surrounds the ability of the wood boring isopod, Sphaeroma terebrans, to burrow into the living prop roots of the red mangrove. Rehm and Humm (1973) were the first to attribute apparently extensive damage of red mangroves stands within the Ten Thousand Islands area of southwestern Florida to an isopod, Sphaeroma. They found extensive damage throughout southwest Florida, some infestation north to Tarpon Springs, and a total lack of infestation in the Florida Keys from Key Largo south to Key West. The destruction process was described as follows: the adult isopod bored into the prop roots (5-mm diameter hole); this was followed by reproduction within the hole and development of juveniles within the root. This process, combined with secondary decomposition from fungi and bacteria, frequently results in prop root severance near the mean high tide mark. These authors attributed loss of numerous prop roots and, in some cases, loss of entire trees during storms to isopod damage.

The extent of damage in the Ten Thousand Islands region led Rehm and Humm (1973) to term the phenomenon an "ecocatastrophe" of possibly great importance. They further stated that shrinking of mangrove areas appeared to be occurring as a result of Sphaeroma infestation; this point was not documented.

Enright (1974) produced a tongue-in-cheek rebuttal, on behalf of Sphaeroma and against the "terrestrial invader", red mangroves. Snedaker (1974) contributed a more substantial argument in which he pointed out that the isopod infestation might be an example of a long-term ecosystem control process.

Further arguments against the "ecocatastrophe" theory were advanced by Estevez and Simon (1975) and Estevez (1978). They provided more life history information for Sphaeroma and suggested a possible explanation for the apparently destructive isopod infestations. They found two species of isopods inhabiting red mangrove prop roots, S. terebrans and a sympatric congener, S. quadridentatum. The latter does not appear to be a wood borer but utilizes S. terebrans burrows. Neither species appeared to utilize mangrove wood as a food source. Estevez and Simon (1975) found extensive burrowing into seedlings in addition to prop root damage. In general, infestations appeared to be patchy and limited to the periphery of mangrove ecosystems. In areas with the highest density of burrows, 23% of all prop roots were infested. There appeared to be more colonization by S. terebrans in regions with full strength sea water (30 to 35 ppt).

The most important finding by Estevez and Simon (1975) and Estevez (1978) was that periods of accelerated activity by S. terebrans were related to periods of fluctuating and slightly increased salinity. This suggests that fluctuations in isopod burrowing may be related to the magnitude of freshwater runoff from the Everglades. These authors agree with Snedaker (1974) and suggest that root and tree loss due to Sphaeroma activity may be beneficial to mangrove ecosystems by accelerating production and root germination. Simberloff et al. (1978) amplified this last suggestion by showing that root branching, which is beneficial to individual trees, is stimulated by isopod activity.

This ecocatastrophe versus beneficial stimulus argument is not completely resolved. Probably, *Sphaeroma* root destruction, in areas of low isopod density, can be a beneficial process to both the individual tree and to the entire mangrove stand. Whether changes in freshwater runoff have accelerated this process to the point where unnatural and widespread damage is occurring is not clear. The data and research perspective to answer this question do not exist. As a result, we are reduced to providing hypotheses which cannot be tested with available knowledge.

2.8 MANGROVE DISEASES

Published research on mangrove diseases is rare. The short paper by Olexa and Freeman (1975) is the principal reference for diseases of Florida mangroves. They reported that black mangroves are affected by the pathogenic fungi, *Phyllosticta hibiscina* and *Nigrospora sphaerica*. These authors found that *P. hibiscina* caused necrotic lesions and death of black mangrove leaves. They felt that under conditions of high relative humidity coupled with high temperatures, this fungus could pose a serious threat to individual trees, particularly if the tree had been weakened by some other natural agent, such as lightning or wind damage. *Nigrospora sphaerica* was considered to be of little danger to black mangroves. Another fungus, *Cylinrocarpon didymum*, appears to form galls on the prop roots and stems of red mangroves. Olexa and Freeman (1975) noted mortality of red mangroves in areas of high gall infestations, although a direct causation link was not proven.

Further research on mangrove diseases is badly needed. Viral disease must be investigated. The role of pathogens in litter production and as indicators of mangrove stress may be very important.

CHAPTER 3. ECOSYSTEM STRUCTURE AND FUNCTION

3.1 STRUCTURAL PROPERTIES OF MANGROVE FORESTS

Published information about the structural aspects of Florida mangrove forests is limited; most existing data have been published since the mid-1970's. This lack of information is unfortunate since quantitative structural data greatly aid understanding of processes such as succession and primary production. Even more important, the response of mangrove forests to stress, both climatic and man-induced, can be followed quantitatively with this type of data.

Ball (1980) contributed substantially to understanding the role of competition in mangrove succession by measuring structural factors such as basal area, tree height, and tree density. Lugo and Zucca (1977) monitored the response of mangrove forests to freezing temperatures by observing changes in structural properties of the trees.

Baseline studies of forest structure have been published by Lugo and Snedaker (1975), and Pool, Snedaker and Lugo (1977). For example, Lugo and Snedaker (1975) compared a fringing mangrove forest and a basin forest at Rookery Bay, near Naples, Florida. They found the fringing forest, which was dominated by red mangroves, to have a tree diversity of H = 1.48, a basal area of 15.9 m^2/ha, an aboveground biomass of 17,932 g/m^2, and a non-existent litter layer. The nearby basin forest was dominated by black mangroves, had a tree diversity of H = 0.96 and a basal area of 23.4 m^2/ha. The litter layer in the basin forest averaged 550 dry g/m^2. Tree diversity in a hurricane disturbed section of the Rookery Bay forest was 1.62. Similar data were presented for mangrove forests in the Ten Thousand Islands area (Table 2).

Data of this type are useful for many purposes including impact statements, environmental surveys, and basic scientific questions. Cintron et al. (1978) gave an indication of the direction in which future research might proceed. Working in a mangrove stand in Puerto Rico, they found tree height to be inversely proportional (r = 0.72) to soil salinity in the range 30 to 72 ppt. Above 55 ppt salinity, dead tree basal area was higher than live tree basal area and above 90 ppt there was no live tree basal area.

It should be possible to investigate the relationship between a variety of mangrove structural properties and factors such as flushing frequency, soil depth, nutrient availability, pollution stress, and other measures of human impact. Ultimately, this should lead to an ability to predict the form and structure of mangrove forests resulting from various physical conditions or artificial impacts. One example of this potential tool is Ball's (1980) documentation of structural changes in mangrove forests resulting from alterations in the hydrological conditions of south Florida.

3.2 ZONATION, SUCCESSION AND "LAND-BUILDING"

Much of the world's mangrove literature consists of descriptive accounts of zonation in mangrove forests and the species composition within these zones. Although general agreement has been lacking, various hypotheses have been put forth concerning the possible connection between zonation, ecological succession, competition, and the role of physical factors such as soil salinity and tidal amplitude. In this section we review briefly the dominant ideas about mangrove zonation and succession and present our interpretation of the current status of knowledge.

Davis (1940), working in south Florida, was one of the first investigators to describe distinct, almost monospecific, zones within mangrove ecosystems. In what has become the classical view, he argued that mangrove zonation patterns were equivalent to seral stages in succession. The most seaward zone, dominated by red mangroves, was regarded as the "pioneer stage". More landward zones were dominated by white mangrove, black mangrove, buttonwood and, finally, the climatic climax, a tropical forest. Since

Table 2. Aboveground biomass of mangrove forests in the Ten Thousand Islands region of Florida. Values are based on 25 m^2 clearcuts and are expressed in dry kg/ha. Data are from Lugo and Snedaker (1975).

Compartment	Scrub mangroves	Overwash mangroves		Fringe mangroves			Riverine mangroves	
Site		A	B	A	B	C	A	B
Leaves	712	7,263	6,946	5,932	5,843	7,037	3,810	9,510
Fruit & flowers	no data	20	236	28	210	131	148	1
Wood	3,959	70,380	70,480	57,960	84,270	128,510	79,620	161,330
Prop roots	3,197	51,980	41,920	22,270	27,200	17,190	14,640	3,060
Litter	1,140	17,310	13,990	22,730	60,250	98,410	42,950	33,930
Total aboveground biomass	9,008	146,953	133,572	108,920	177,773	251,278	141,168	207,831

these zones were regarded as progressively later stages in succession, the entire mangrove ecosystem was believed to be moving seaward through a process of sediment accumulation and colonization. Davis based his argument primarily upon the sequence of observed zones and cores which showed red mangrove peat underlying black mangrove peat which, in turn, occurred under terestrial plant communities.

Unfortunately, this Clementsian interpretation of mangrove zonation was widely accepted, but rarely tested. For example, Chapman (1970) expanded Davis' original successional concept from south Florida to explain zonation in mangrove forests in other parts of the world. Walsh (1974) thoroughly reviewed the mangrove succession/zonation literature.

Fortunately, not everyone accepted Davis' point of view. Egler (1952) and later Thom (1967, 1975) argued that mangrove zonation was a response to external physical forces rather than temporal sequence induced by the plants themselves. Egler (1952) showed that patterns of sediment deposition predicted by Davis' (1940) theory did not always occur. He also showed that in some cases mangrove zones appeared to be moving landward rather than seaward. Sea level has been rising in south Florida at the rate of 1 ft (30 cm) per 100 to 150 years (Provost 1974). Spackman et al. (1966) emphasized the role of sea level change in determining changes in mangrove zonation, both through sea level rise and land subsidence. Both Egler (1952) and Spackman et al. (1966) along with Wanless (1974) and Thom (1967, 1975) suggested that mangroves were reacting passively rather than actively to strong geomorphological processes. This implies that mangroves should be regarded as "land-stabilizers" rather than "land-builders".

Furthermore, field researchers frequently noted that red mangroves were not always the only "pioneer species" on recently deposited sediment. It is not unusual to find seedlings of black, white, and red mangroves growing together on a new colonization site. Lewis and Dunstan (1975) found that black mangroves and white mangroves along with the saltmeadow cordgrass, *Spartina patens*, are often the pioneers on new dredge spoil islands in central Florida. On the northern coast of the Gulf of Mexico, where black mangrove is the only mangrove species present, it may be preceded by marsh grasses such as saltmarsh cordgrass, *S. patens*, smooth cordgrass, *S. alterniflora*, or the black needle rush, *Juncus roemerianus*. In Puerto Rico, we observed that white mangrove often pioneers and dominates sites where oceanic overwash of beach sand has occurred. All of these observations detract from Davis' (1940) original contention that red mangroves should be regarded as the initial colonizer of recently deposited sediments. It appears that under certain conditions, e.g., shallow water depths, substrate type, and latitude, white and black mangroves or marsh grasses can be effective pioneer species.

The work of Rabinowitz (1975) added a new perspective to the mangrove zonation debate. Through carefully designed reciprocal planting experiments in Panamanian mangrove forests using species of *Rhizophora*, *Laguncularia*, *Pelliciera* and *Avicennia*, she demonstrated that each species could grow well within any of the mangrove zones. In other words, physical and chemical factors such as soil salinity or frequency of tidal inundation, within each zone, were not solely responsible for excluding species from that zone. To explain zonation, Rabinowitz proposed tidal sorting of propagules based upon propagule size, rather than habitat adaptation,as the most important mechanism for zonation control.

The most recent piece to be added to the zonation/succession puzzle comes from the work of Ball (1980). Based upon research of mangrove secondary succession patterns adjacent to Biscayne Bay, Florida, she made a strong case for the importance of interspecific competition in controlling zonation. She found that white mangroves, which grow best in intertidal areas, do not occur consistently in the intertidal zone of mature mangrove stands. Instead, white mangroves dominate higher, drier locations above mean high water where the red mangrove does not appear to have a competitive advantage. She suggested that competition is not so important during the early stages of succession but becomes critical as individual trees reach maturity and require more space and other resources.

Inherent in Ball's concept of zonation is the differential influence of physical factors (e.g., soil salinity, depth to water table) on the competitive abilities of the different mangrove species. She concluded that succession proceeds independently within each zone, although breaks in the forest canopy from lightning strikes or high winds may produce a mosaic of different successional stages within a zone. These openings allow species whose seedlings do not compete well in shade, such as the white mangrove, to become established, at least temporarily, within solid zones of red mangroves.

Zonation of mangrove species does not appear to be controlled by physical and chemical factors directly, but by the interplay of these factors with interspecific competition and, possibly, through tidal sorting of propagules. Once succession in a mangrove zone reaches an equilibrium state, change is unlikely unless an external perturbation occurs. These perturbations range from small-scale disturbance (lightning strikes) to large-scale perturbations (sea level change, hurricane damage) and may cause succession within zones to regress to an earlier stage. There is some evidence in south Florida that hurricane perturbations occur on a fairly regular basis, creating a pattern of cyclical succession.

Except for Ball (1980) and Taylor (1980), the importance of fires as an influence on mangrove succession has been generally ignored. Most fires in the Florida mangrove zone are initiated by lightning and consist of small circular openings in the mangrove canopy (Taylor 1980). These openings present an opportunity for secondary succession within an established zone. For example, we have frequently observed white mangroves flourishing in small lightning-created openings in the center of red mangrove forests. Fire may also play a role in limiting the inland spread of mangroves. Taylor (1981) pointed out that Everglades fires appear to prevent the encroachment of red and white mangroves into adjacent herbaceous communities.

Finally, Lugo and Snedaker (1974), Cintron et al. (1978) and Lugo (1980) suggested that mangrove ecosystems function as classical successional systems in areas of rapid sediment deposition or upon recently colonized sites such as offshore islands. They concluded that in most areas mangrove forests are an example of steady-state cyclical systems. Conceptually, this is synonymous to E. P. Odum's (1971) cyclic or catastrophic climax. Chapman (1976a, b) suggested the idea of cyclic succession for a variety of coastal ecosystems.

If Florida mangrove ecosystems are cyclic systems, then there should be an identifiable perturbation capable of setting succession back to an early stage. Lugo and Snedaker (1974) suggested that hurricanes may play this role. They pointed out (without substantiating data) that major hurricanes occur about every 20-25 years in south Florida. Coincidently, mangrove ecosystems appear to reach their maximum levels of productivity in about the same period of time (Lugo and Snedaker 1974). This hypothesis suggests that succession within many mangrove ecosystems may proceed on a cyclical basis rather than in the classical fashion. Possibly other physical perturbations may influence mangrove succession including incursions of freezing temperatures into central Florida, periodic droughts causing unusually high soil salinities (Cintron et al. 1978), and fire spreading into the upper zones of mangrove forests from terrestrial sources.

Although understanding of zonation and succession in mangrove ecosystems remains incomplete, a clearer picture is emerging, at least for south Florida. Contrary to early suggestions, mangrove species zonation does not appear to represent seral stages of succession except, perhaps, for locations of recent colonization or where sediment is accumulating rapidly. The role of mangroves in land-building seems more passive than active. Geomorphological and hydrological processes appear to be the dominant forces in determining whether mangrove shorelines recede or grow. The role of mangroves is to stabilize sediments which have been deposited by physical processes.

3.3 NUTRIENT CYCLING

Current understanding of nutrient cycles in mangrove ecosystems is far from satisfactory. Sporadic field measurements have been made, but a complete nutrient budget has not been published for any mangrove ecosystem in the world.

Several pioneering field studies were conducted in Florida (Carter et al. 1973; Snedaker and Lugo 1973; Onuf et al. 1977) and one simulation model of mangrove nutrient cycling has been published (Lugo et al. 1976). Preliminary measurements of nitrogen fixation were made (Zuberer and Silver 1975; Gotto and Taylor 1976; Zuberer and Silver 1978; Gotto et al. 1981). Based on these studies, we present the following preliminary conclusions.

Mangrove ecosystems tend to act as a sink (net accumulator) for various elements including macro nutrients such as nitrogen and phosphorus, trace elements, and heavy metals. As we have discussed in section 1.7, these elements are removed from waters flowing through mangrove swamps by the concerted action of the mangrove prop roots, prop root algae, the associated sediments, the fine root system of the mangrove trees, and the host of small invertebrates and microorganisms attached to all of these surfaces. Although the turnover times for these elements in mangrove swamps are not known, it appears that at least a portion may be stored or tied up in wood, sediments, and peat for many years.

Although mangrove ecosystems may tend to accumulate nutrients, there is a continual loss through export of particulate and dissolved substances. If significant nutrient storage and resultant high primary production are to occur, there must be a continual input of nutrients to the mangrove forest from outside the system (Figure 7). Where nutrient influx to the mangrove ecosystem is approximately balanced by nutrient loss in exported organic matter, then nutrient storage will be minimal and mangrove net primary production will be low. This appears to occur in the scrub mangrove community type and to a lesser extent in the basin and hammock community types.

Carter et al. (1973) and Snedaker and Lugo (1973) have hypothesized that the greatest natural nutrient inputs for mangrove swamps come from upland and terrestrial sources. Apparently for this reason, the most luxuriant and productive mangrove forests in south Florida occur in riverine locations or adjacent to significant upland drainage.

Localized sources of nutrients, such as bird rookeries, can result in greater nutrient storage and higher mangrove productivity (Onuf et al. 1977). If however, large bird rookeries (or artificial nutrient inputs) occur in poorly flushed sections of mangrove ecosystems, resultant high nutrient levels may inhibit mangrove growth (R. R. Lewis, III, Hillsborough Community College, Tampa, Fla.; personal communication 1981).

The output from the simulation model of Lugo et al. (1976) suggests that if nutrient input to a mangrove ecosystem is reduced, then nutrient storage levels within the mangrove ecosystem will be reduced and mangrove biomass and productivity will decline. To our knowledge this hypothesis has not been tested in the field.

Nitrogen fixation occurs in mangrove swamps at rates comparable to those measured in other shallow, tropical marine areas (Gotto et al. 1981). Nitrogen

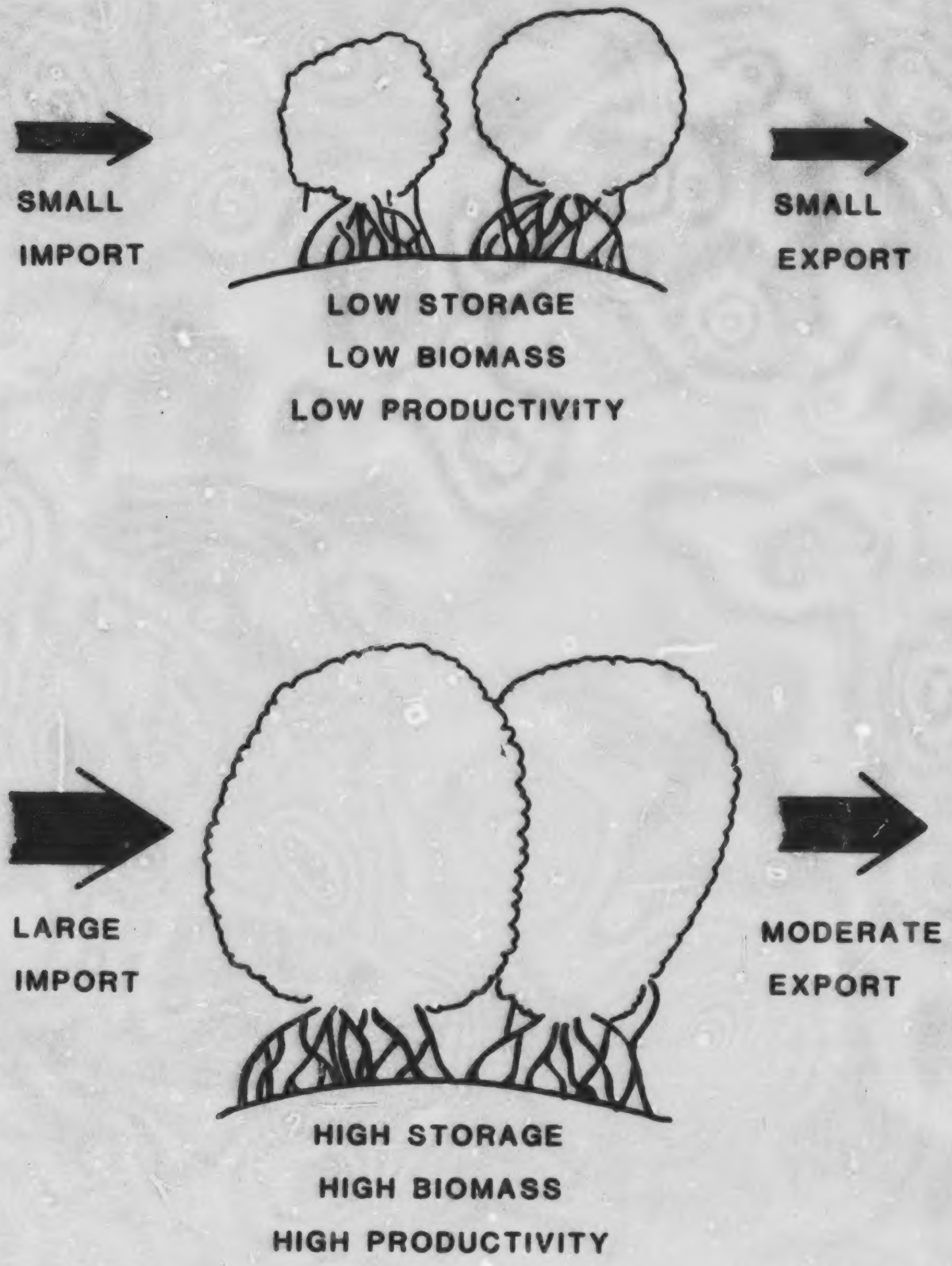

SMALL
IMPORT
SMALL
EXPORT
LOW STORAGE
LOW BIOMASS
LOW PRODUCTIVITY
LARGE
IMPORT
MODERATE
EXPORT
HIGH STORAGE
HIGH BIOMASS
HIGH PRODUCTIVITY

Figure 7. The hypothetical relationship between nutrient input (excluding carbon), biomass, primary productivity, and nutrient export (including carbon) from mangrove ecosystems. Top: small nutrient import. Bottom: large nutrient import.

fixation has been found in association with mangrove leaves, both living and dead, mangrove sediment surfaces, the litter layer in mangrove swamps, and mangrove root systems (Gotto and Taylor 1976; Zuberer and Silver 1978; Gotto et al. 1981). In virtually all cases, nitrogen fixation appears to be limited by the availability of labile carbon compounds. Perhaps for this reason, the highest rates of mangrove nitrogen fixation have been measured in association with decaying mangrove leaves; presumably, the decaying leaves act as a carbon source and thus accelerate nitrogen fixation. Macko (1981), using stable nitrogen ratio techniques, has indicated that as much as 25% of the nitrogen associated with black mangrove peat in Texas is derived from nitrogen fixation.

Zuberer and Silver (1978) speculated that the nitrogen fixation rates observed in Florida mangrove swamps may be sufficient to supply a significant portion of the mangrove's growth requirements. Although this hypothesis is impossible to test with present information, it might explain why moderately productive mangrove stands occur in waters which are severely nitrogen depleted.

In summary, knowledge of nutrient cycling in mangrove swamps is highly speculative. These ecosystems appear to act as a sink for many elements, including nitrogen and phosphorus, as long as a modest input occurs. Nitrogen fixation within the swamp may provide much of the nitrogen needed for mangrove growth.

3.4 LITTER FALL AND DECOMPOSITION

Unless otherwise stated, litter fall refers to leaves, wood (twigs), leaf scales, propagules, bracts, flowers, and insect frass (excrement) which fall from the tree. Mangrove leaves are shed continuously throughout the year although a minor peak occurs during the early part of the summer wet season in Florida (Heald 1969; Pool et al. 1975). Sporadic litter fall peaks may follow periods of stress from cold air temperatures, high soil salinities, and pollution events. Litter fall typically can be partitioned as 68% to 86% leaves, 3% to 15% twigs and 8% to 21% miscellaneous; the latter includes flowers and propagules.

Litter fall is an important ecosystem process because it forms the energy basis for detritus-based foodwebs in mangrove swamps (see sections 3.5 and 3.6). The first measurements of litter fall in mangrove swamps were made by E.J. Heald and W.E. Odum, working in the North River estuary in south Florida in 1966-69. This was subsequently published as Heald (1969), Odum (1970), and Odum and Heald (1975a). They estimated that litter production from riverine red mangrove forests averaged 2.4 dry g of organic matter/m^2/day (or 876 g/m^2/year or 8.8 metric tons/ha/year).

Subsequent studies agreed with this early estimate (Table 3), although variation clearly exists between different types of communities. Scrub forests with scattered, very small trees have the smallest amount of leaf fall. Basin and hammock forests, which appear to be nutrient limited, have intermediate leaf fall values. Not surprisingly, the highest values occur in the highly productive fringing, overwash, and riverine forests. Odum and Heald (1975a) suggested that the relatively uniform litter fall values from productive mangrove forests around the world result from the shade intolerance of the canopy leaves and the tendency for the canopy size to remain the same in spite of increasing height. If detailed information is lacking, red mangrove forests of south Florida, which are not severely limited by lack of nutrients, can be assumed to produce litter fall of 2.0 to 3.0 g/m^2/day of dry organic matter. Pure stands of black mangroves usually have a lower rate of 1.0 to 1.5 g/m^2/day (Lugo et al. 1980).

Decomposition of fallen Florida mangrove leaves has been investigated by a number of researchers including Heald (1969), Odum (1970), Odum and Heald (1975a), Pool et al. (1975), Lugo and Snedaker (1975), Twilley (1980) and Lugo et

Table 3. Estimates of litter fall in mangrove forests. Total litter fall includes leaves, fruits, twigs, flowers, and bark. R = red mangrove, W = white mangrove, B = black mangrove.

Species	Leaf fall ($g/m^2/day$)	Total litter fall ($g/m^2/day$)	Annual litter fall (metric tons/ha/yr)	Reference
R (riverine)	1.3	2.4	8.8	Heald 1969
R (riverine)	---	3.6	12.8	Pool et al. 1975
R (overwash)	---	2.7	9.9	Pool et al. 1975
R (fringe)	---	2.7	9.9	Pool et al. 1975
R,B (basin)	---	2.0	7.3	Pool et al. 1975
R (mature)	2.2	2.9	10.6	Teas 1979
R (scrub)	0.2	0.4	1.3	Teas 1979
B (basin)	0.7	0.8	2.9	Teas 1979
B (basin)	---	2.2	8.0	Courtney 1980
B	---	1.3	4.9	Twilley 1980
B	---	1.3	4.8	Lugo et al. 1980
Mixed R,B,W	---	2.5	9.0	Lugo et al. 1980
B	---	0.8	2.9	Pool et al. 1975
Variety of community types	---	0.8 - 2.1	2.9 - 7.7	Heald et al. 1979
26 species (Australia)	---	2.4	8.8	Boto & Bunt (MS. in prep.)

al. (1980). Heald and Odum showed that decomposition of red mangrove leaves proceeds most rapidly under marine conditions, somewhat more slowly in freshwater, and very slowly on dry substrates. For example, using the litter bag method, they found that only 9% of the original dry weight remained after 4 months in sea water. By comparison, 39% and 54% remained at the end of comparable periods in brackish water and freshwater. Under dry conditions, 65% remained. Higher decomposition rates in sea water were related to increased activity of shredder organisms, such as crabs and amphipods.

Heald (1969) and Odum (1970) also found increases in nitrogen, protein, and caloric content as mangrove leaves progressively decayed. The nitrogen content of leaves decaying under brackish conditions (on an AFDW basis) increased from 1.5% (5.6% protein) to 3.3% (20.6% protein) over a 6-month period. Subsequent information (Odum et al. 1979b) suggested that the protein increase may not have been this great since some of the nitrogen increase probably included non-protein nitrogen compounds such as amino sugars. Fell and Master (1973), Fell et al. (1980), Fell and Newell (1980), and Fell et al. (1980) have provided more detailed information on red mangrove leaf decomposition, the role of fungi in decomposition (see section 4), and nitrogen changes and nitrogen immobilization during decomposition. Fell et al. (1980) have shown that as much as 50% of weight loss of the leaf during decomposition is in the form of dissolved organic matter (DOM).

Heald et al. (1979), Lugo et al. (1980) and Twilley (1980) discovered that black mangrove leaves decompose more rapidly than red mangrove leaves and apparently produce a higher percentage of DOM. Pool et al. (1975) have shown that mangrove litter decomposes and is exported most rapidly from frequently flooded riverine and overwash forests. These communities have little accumulation of litter on the forest floor. Communities which are not as well-flushed by the tides, such as the basin and hammock forests, have slower rates of decomposition and lower export rates.

3.5 CARBON EXPORT

Research from Florida mangrove swamps forms a small portion of the larger controversy concerned with the extent to which coastal wetlands export particulate organic carbon (reviewed by Odum et al. 1979a). Available evidence from Florida, Puerto Rico and Australia (Table 4) suggests that mangrove swamps tend to be net exporters. The values in Table 4 should be regarded as preliminary, however, since all five studies are based upon simplistic assumptions and methodology.

Golley et al. (1962) based their annual estimate of particulate carbon export from a Puerto Rican forest upon a few weeks of measurements. Odum and Heald's estimates were derived from two or three measurements a month. All investigators have ignored the importance of bed load transport and the impact of extreme events. All investigators except Lugo et al. (1980) have failed to measure DOC flux.

It seems relatively clear that mangrove forests do export organic carbon to nearby bodies of water. The magnitude of this export has probably been underestimated due to ignoring bedload, extreme events, and DOC.

The value of this carbon input to secondary consumers in receiving waters is not clear. As shown in section 3.6, food webs based primarily upon mangrove carbon do exist. The relative importance of mangrove carbon to Florida coastal ecosystems remains speculative. We suspect that mangrove-based food webs are dominant in small bays, creeks and rivers within large mangrove ecosystems such as the North River system studied by Heald (1969) and Odum (1970). In intermediate-sized bodies of water, such as Rookery Bay near Naples, Florida, mangroves are probably important but not dominant sources of organic carbon. Lugo et al. (1980) estimate that mangroves supply 32% of the organic carbon

Table 4. Estimates of particulate carbon export from mangrove forests. Lugo et al. (1976) estimated export from a theoretical, steady state forest using a simulation model. Lugo et al. (1980) measured export from an inland black mangrove forest.

Investigators	Location	Export	
		$g/m^2/day$	tonnes/ha/yr
Golley et al. (1962)	Puerto Rico	1.1	4.0
Heald (1969), Odum (1970)[a]	Florida	0.7	2.5
Lugo and Snedaker (1975)	Florida	0.5	2.0
Lugo et al. (1976)	Florida	1.5 - 1.8	5.5 - 6.6
Boto and Bunt (1981)	Australia	1.1	4.0
Lugo et al. (1980)[b]	Florida	0.2	0.7

[a] Estimate only includes carbon of mangrove origin.
[b] Estimate includes dissolved and particulate carbon.

input to Rookery Bay. In very large systems, such as Biscayne Bay near Miami, Florida, mangroves are clearly less important than any other sources such as algae and sea grasses, although mangrove carbon may be important in localized situations such as the immediate vicinity of fringing and overwash forests. The magnitude of mangrove carbon export to unenclosed coastal waters and offshore remains a mystery.

3.6 ENERGY FLOW

At least seven sources of organic carbon may serve as energy inputs for consumers in mangrove ecosystems (Figure 8). The pathways by which this energy containing material is processed and made available to each consumer species is indeed complex. Not surprisingly, current understanding of energy flow in Florida mangrove ecosystems exists largely in a qualitative sense; quantitative data are scarce and piecemeal. A variety of investigators have contributed information over the past decade including, but not limited to, Heald (1969), Odum (1970), Odum and Heald (1972), Carter et al. (1973), Snedaker and Lugo (1973), Heald et al. (1974), Lugo and Snedaker (1974, 1975), Odum and Heald (1975a, b), and Pool et al. (1977). Probably, the most complete study to date is the investigation of energy flow in the black mangrove zone of Rookery Bay by Lugo et al. (1980).

It is possible at this time to present a series of hypotheses concerning the relative importance of these energy sources. First, the relative importance of each source can vary from one location to the next. As will be shown in the following discussion, the consumers in certain mangrove forests appear to depend primarily upon mangrove-derived carbon while in other locations inputs from phytoplankton and attached algae are probably more important.

Our second hypothesis is that energy flow based upon phytoplankton is most important in overwash mangrove forests and other locations associated with large bodies of clear, relatively deep water. Conversely, phytoplankton are hypothesized to be relatively unimportant to the energy budgets of the large riverine forest communities along the southwest coast of Florida. It should be remembered, however, that even where phytoplankton are quantitatively unimportant, they potentially perform an important function as the basis of phytoplankton-zooplankton-larval fish food webs (Odum 1970).

As a third hypothesis, Iver Brook (Rosensteil School of Marine and Atmospheric Sciences, Rickenbacker Causeway, Miami, Fla.; personal communication 1979) has suggested that both sea grasses and benthic algae serve as an important energy source for fringing mangrove communities adjacent to large bodies of water such as Biscayne Bay and Whitewater Bay. Although little evidence exists to test this hypothesis, observations of extensive deposits of sea grass and macroalgal detritus within mangrove forests suggest intuitively that Brook's hypothesis may be correct.

In regions where mangrove shading of the prop roots is not severe, our fourth hypothesis suggests that carbon originating from prop root epiphytes may be significant to community energy budgets. Lugo et al. (1975) have measured net production of periphyton in mangroves fringing Rookery Bay and found average values of 1.1 $gC/m^2/day$. Hoffman and Dawes (1980) found a lower value of 0.14 $gC/m^2/day$. Because these values are roughly comparable to average exports of mangrove leaf carbon (section 3.5), its potential importance is obvious.

The fifth hypothesis states that mangrove organic matter, particularly leaf material, is an important energy source for aquatic consumers. This hypothesis was first espoused by Heald (1969) and Odum (1970), who worked together in the riverine mangrove communities between the Everglades and Whitewater Bay. Clearly, mangrove carbon is of great importance within the riverine and basin communities all along the southwest coast of Florida (Odum and Heald 1975b); Carter et al. (1973) and Snedaker and Lugo (1973)

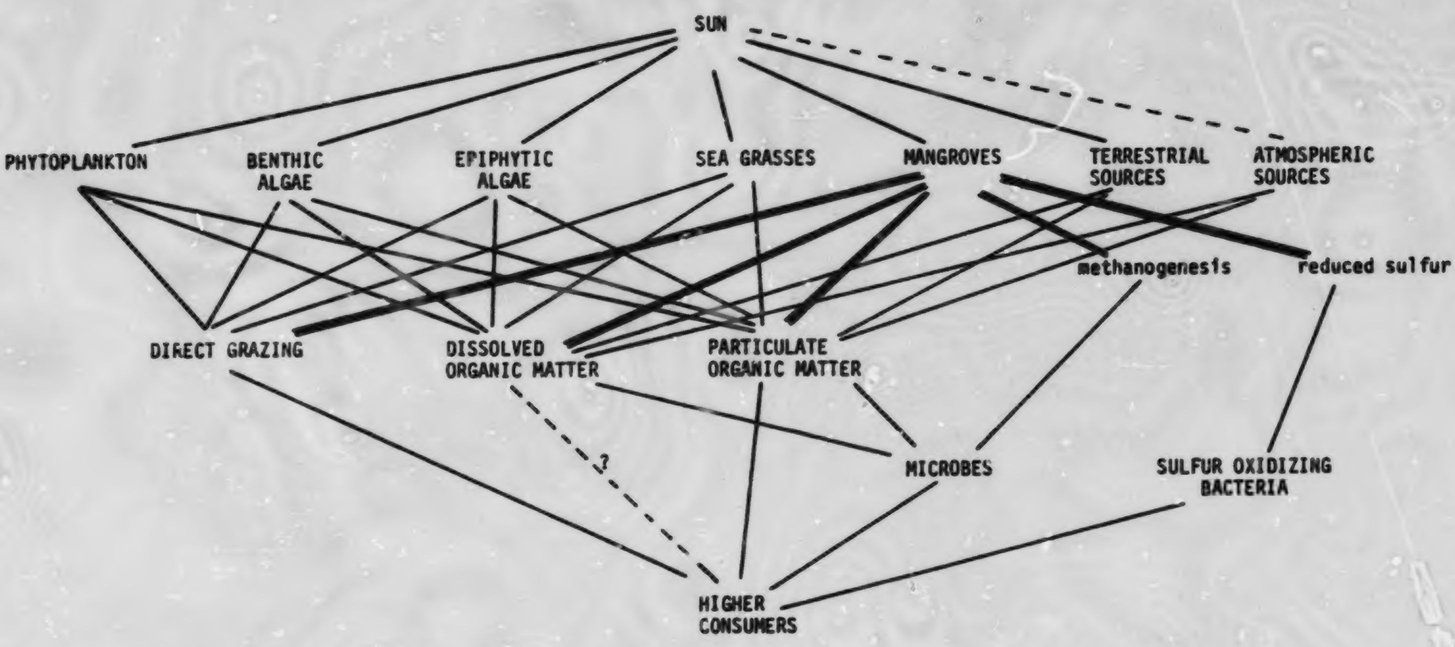

SUN
PHYTOPLANKTON
BENTHIC ALGAE
EPIPHYTIC ALGAE
SEA GRASSES
MANGROVES
TERRESTRIAL SOURCES
ATMOSPHERIC SOURCES
methanogenesis
reduced sulfur
DIRECT GRAZING
DISSOLVED ORGANIC MATTER
PARTICULATE ORGANIC MATTER
?
MICROBES
SULFUR OXIDIZING BACTERIA
HIGHER CONSUMERS

Figure 8. Potential pathways of energy flow in mangrove ecosystems. Not all possible pathways have been drawn; for example, methanogenesis and sulfur reduction could originate from any of the sources of organic matter. Mangrove-based pathways are enhanced for emphasis and in no way imply relative importance.

provided subsequent supportive data. What is not clear, is the relative importance of mangrove carbon to consumers within fringing, overwash, and more isolated mangrove communities.

Our sixth hypothesis involves the assemblage of organisms that graze mangrove leaves directly. A variety of insects (see section 6) and the mangrove tree crab, Aratus pisonii, (Beever et al. 1979) obtain much of their energy directly from living mangrove leaves, even though grazing rarely exceeds 10% of net primary production (Odum and Heald 1975b).

As a seventh hypothesis we suggest that anaerobic decomposition of mangrove tissue, particularly root material, may support an extensive food web based on bacteria associated with methanogenesis or the processing of reduced sulfur compounds. Our suggestion of the importance of reduced sulfur comes directly from Howarth and Teal's (1980) discovery of this potentially important energy pathway in temperate Spartina (cordgrass) marshes. They found that anaerobic decomposition is such an incomplete process that if sulfates are available (from sea water) as much as 75% of the original energy in plant tissues may be converted by sulfur reducing bacteria to reduced sulfur compounds such as hydrogen sulfide and pyrite. Subsequently, if these reduced sulfur compounds are moved hydrologically to an oxidized environment (sediment surface or creek bank) sulfur-oxidizing bacteria (e.g., Thiobacillus spp.) may convert the chemically stored energy to bacterially stored energy with an efficiency as great as 50% (Payne 1970). Presumably, deposit-feeding organisms such as grass shrimp (Palaemonetes) and mullet (Mugil) are capable of grazing these sulfur-oxidizing bacteria from the sediment surface. If this hypothetical trophic exchange does exist, it may be of considerable magnitude and may cause us to reexamine current concepts of energy processing and export from mangrove ecosystems. Since freshwater contains remarkably little sulfate in comparison to seawater, this energy pathway is probably of little importance in mangrove forests of very low salinity.

Carbon inputs from terrestrial sources may be important to certain mangrove communities. Carter et al. (1973) have shown that terrestrial carbon can reach coastal ecosystems particularly where man has cut deep channels inland for navigation or drainage purposes. The magnitude of this influx has not been adequately measured although Carter et al. did find that mainland forests (including mangroves) contributed approximately 2,100 metric tons of carbon per year to Fahkahatchee Bay.

Atmospheric inputs from rainfall appear to be minimal in all cases. Lugo et al. (1980) measured throughfall (precipitation passing through the tree canopy) in Rookery Bay mangrove forests of 15 to 17 gC/m^2/year. This would be an overestimate of atmospheric input since it contains carbon leached from mangrove leaves. The best guess of atmospheric input is between 3 to 5 gC/m^2/year for south Florida mangrove ecosystems.

Subsequent stages of energy transfer in mangrove community food webs remain largely hypothetical. Odum (1970) and Odum and Heald (1975b) have outlined several pathways whereby mangrove carbon and energy are processed by a variety of organisms (see Figure 8). Apparently, the most important pathway follows the sequence: mangrove-leaf detritus substrate-microbe-detritus consumer-higher consumers. The critical links are provided by the microbes such as bacteria and fungi (see Fell et al. 1975) and by the detritus consumers. The latter group was studied by Odum (1970) and Odum and Heald (1975b) and found to consist of a variety of invertebrates (e.g., caridean shrimp, crabs, mollusks, insect larvae, amphipods) and a few fishes.

Stable carbon studies such as those done by Haines (1976) in Spartina (cordgrass) marshes have not been performed in mangrove ecosystems. Mangroves are C_3 plants and have δ^{13} values in the range of minus 25 to minus 26 (Macko 1981). According to the same author, mangrove peat has a δ^{13} value of minus 22. Because these values are dramatically different from the values for sea grasses and many algae, the possibilities for using this tool in mangrove ecosystems is excellent. Macko (1981) also suggested the utility of using stable nitrogen ratios for future mangrove food web investigations; he reported δ^{15} values of plus 6.0 to plus 6.5 for mangrove tissue and plus 5 for mangrove peat.

In reviewing contemporary knowledge of energy flow in mangrove ecosystems, three conclusions emerge.

(1) We have a hypothetical framework of mangrove energy flow of a qualitative nature. This framework appears to be reasonably accurate although subsequent developments, such as elucidation of the reduced sulfur hypothesis, may require some modification.

(2) Measurements of the relative importance of various carbon sources are generally lacking.

(3) Detailed measurements of energy flow including the relative inputs of different carbon sources are critically needed. Technological difficulties, high costs, and difficulties inherent in transferring findings from one estuary to the next present a major challenge to estuarine ecologists of the future.

CHAPTER 4. COMMUNITY COMPONENTS - MICROORGANISMS

The mycoflora (fungi) are the best studied component of the microbial community of mangrove swamps. Much pioneering work has been carried out in south Florida. Reviews of the current knowledge of mangrove-associated fungi can be found in Kohlmeyer and Kohlmeyer (1979) and Fell et al. (1980).

One of the earliest studies of mangrove mycoflora was published by Kohlmeyer (1969). He discovered large populations of marine fungi on the submerged parts of aerial roots, stems, and branches and on living and dead mangrove leaves. Extensive work at the University of Miami by Fell and his coworkers (e.g., Fell and Master 1973; Fell et al. 1975, 1980) explored the role of fungi in the decomposition of mangrove leaves and the immobilization of nitrogen. Newell (1974) studied the succession of mycoflora on seedlings of red mangrove. A survey of the aquatic yeasts occurring in the south Florida mangrove zone was published by Ahearn et al. (1968).

One of the most interesting pieces of information to emerge from this extensive mycoflora research concerns the succession of organisms associated with decaying leaves (summarized by Fell et al. 1975, 1980). Senescent leaves of red mangroves are typically colonized by species of *Nigrospora*, *Phyllostica*, and *Pestalotica*. Once the leaf has fallen from the tree and during the early stages of decay, the fungal flora is dominated by species of *Phytophthora* and, to a lesser extent, *Drechslera* and *Gloeosporium*. In the latter stages of decay the dominant genera are *Calso*, *Gliocidium*, and *Lulworthia*.

Understanding the occurrence and succession of fungi on decaying mangrove leaves is important because of their role in energy flow in mangrove swamps. Heald (1969), Odum (1970) and Odum and Heald (1975b) hypothesized that fungi and bacteria are important in converting mangrove leaf organic material into a form that can be digested and assimilated by detritivores (see section 3.6).

Our understanding of the role and occurrence of bacteria in mangrove swamps is not as well documented as for fungi. Casagrande and Given (1975) have suggested that bacteria are important in the early stages of mangrove leaf decomposition and are replaced in the latter stages by fungi which are better equipped to attack refractive organic compounds. Unlike the mycoflora, the bacteria are clearly important in the anaerobic regions of mangrove swamps. Vankatesan and Ramamurthy (unpubl. data) found denitrifying bacteria to be abundant and ubiquitous in mangrove soils. Zuberer and Silver (1978) have emphasized the importance of nitrogen-fixing bacteria in the zone around mangrove roots. They, in fact, were able to isolate and count a variety of types of bacteria from mangrove sediments including aerobic heterotrophs, anaerobic heterotrophs, nitrogen-fixing heterotrophs, and sulfate-reducing bacteria.

CHAPTER 5. COMMUNITY COMPONENTS - PLANTS OTHER THAN MANGROVES

5.1. ROOT AND MUD ALGAE

The aerial root systems of mangroves provide a convenient substrate for attachment of algae. These root algal communities are particularly noticeable on red mangrove prop roots but also occur to a lesser extent on black mangrove pneumatophores located in the intertidal zone. Productivity of prop root algal communities can be appreciable if shading by mangroves is not too severe; as discussed in section 3.6, Lugo et al. (1975) found a prop root community net primary production rate of 1.1 gC/m^2/day, a level comparable to mangrove leaf fall. Biomass of these algae can be as high as 200 to 300 g per prop root (Burkholder and Almodovar 1973). Of course, production of this magnitude only occurs on the edge of the forest and is virtually nil in the center of the swamp. Nevertheless, this algal carbon has considerable potential food value either to direct grazers or detritivores.

Vertical distribution of prop root algae has been studied by many researchers (Gerlach 1958; Almodovar and Biebl 1962; Biebl 1962; Post 1963; Rutzler 1969; Burkholder and Almodovar 1973; Rehm 1974; Yoshioka 1975); only one of these studies (Rehm 1974) was conducted in Florida. There is a tendency for certain genera of algae to form a characteristic association on mangrove roots around the world (Post 1963). Four phyla tend to dominate: Chlorophyta, Cyanophyta, Phaeophyta, and Rhodophyta; the last is usually the most important in terms of biomass. Of 74 species of marine algae recorded as prop root epiphytes between Tampa and Key Largo, 38 were Rhodophyta, 29 Chlorophyta, 4 Phaeophyta and 3 Cyanophyta (Rehm 1974).

Zonation to be expected on Florida mangroves is shown in Figure 9; this sequence comes largely from Taylor (1960). Near the high water mark, a green band usually exists which is dominated by species of *Rhizoclonium*. Below this is a zone dominated by species of *Bostrychia*, *Catenella*, and *Caloglossa*. It is this association that most people think of when mangrove prop root algae are mentioned. Because much mud is often deposited on the *Bostrychia*-*Catenella*-*Caloglossa* complex, it often has a dingy, gray appearance. There are many other algae found in this zone, but these three genera usually dominate. At brackish or nearly freshwater locations, they are replaced by species of *Batophora*, *Chaetomorpha*, *Cladophora*, and *Penicillus*. The pneumatophores of *Avicennia*, when colonized, are often covered with species of *Rhizoclonium*, *Bostrychia* and *Monostroma* (Taylor 1960). Hoffman and Dawes (1980) found that the *Bostrychia binderi*-dominated community on the pneumatophores of black mangroves had a standing crop of 22 g dry wt/m^2 and a net production of 0.14 gC/m^2/day.

If there is a permanently submerged portion of the prop root, it may be covered with rich growths of *Acanthophora*, *Spyrida*, *Hypnea*, *Laurencia*, *Wrangelia*, *Valonia*, and *Caulerpa* (Almodovar and Biebl 1962). Additional genera which may be present below mean high water are: *Murrayella*, *Polysiphonia*, *Centroceras*, *Wurdemannia*, *Dictyota*, *Halimeda*, *Laurencia*, and *Dasya* (Taylor 1960; Burkholder and Almodovar 1973; Yoshioka 1975). In addition, anywhere on the moist sections of the prop roots there are usually epiphytic diatoms and filamentous green and blue-green algae of many genera.

Rehm (1974) found a significant difference in the prop root algae between south and central Florida. South of Tampa Bay the standard *Bostrychia*-*Catenella*-*Caloglossa* dominates. In the Tampa Bay area, species of the orders Ulotrichales and Cladophorales are dominant.

The mud adjacent to the mangrove root community is often richly populated with a variety of algae. These can include species of *Cladophoropsis*, *Enteromorpha*, *Vaucheria*, and *Boodleopsis* (Taylor 1960) in addition to a whole host of benthic diatoms and dinoflagellates (Wood 1965) and other filamentous green and blue-green algae (Marathe 1965).

Adjacent to mangrove areas, on the bottoms of shoals, shallow bays and creeks, there is often a variety of

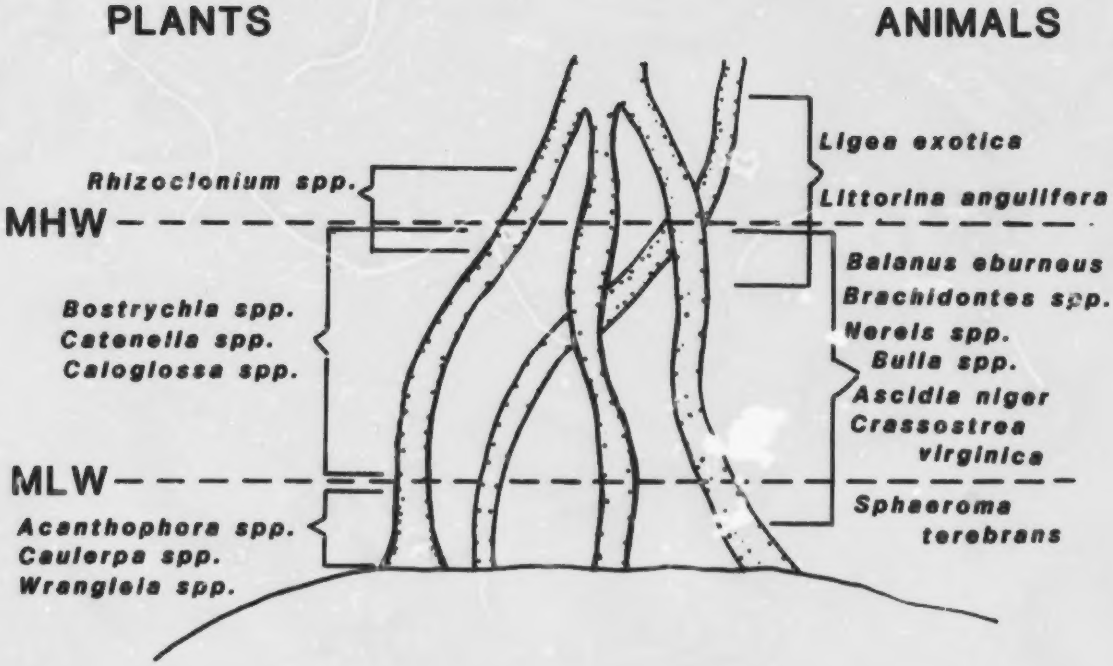

PLANTS
ANIMALS
Ligea exotica
Littorina angulifera
Rhizoclonium spp.
MHW
Balanus eburneus
Brachidontes spp.
Bostrychia spp.
Catenella spp.
Caloglossa spp.
Nereis spp.
Bulla spp.
Ascidia niger
Crassostrea virginica
MLW
Sphaeroma terebrans
Acanthophora spp.
Caulerpa spp.
Wrangleia spp.

Figure 9. Vertical distribution of selected algae and invertebrates on red mangrove prop roots (compiled from Taylor 1960 and our own observations).

tropical algae including species of *Caulerpa*, *Acetabularia*, *Penicillus*, *Gracilaria*, *Halimeda*, *Sargassum*, *Batophora*, *Udotea*, and *Dasya*. These are discussed at length by Zieman (in prep.). Other pertinent references for mangrove regions include Davis (1940), Taylor (1960), Tabb and Manning (1961), and Tabb et al. (1962).

5.2 PHYTOPLANKTON

All aspects of phytoplankton, from seasonal occurrence to productivity studies, are poorly studied in mangrove ecosystems. This is particularly true in Florida.

Evidence from Brazil (Teixeira et al. 1965, 1967, 1969; Tundisi 1969) indicates that phytoplankton can be an important component of the total primary production in mangrove ecosystems; just how important is not clear. Generally, standing crops of net phytoplankton in mangrove areas are low (personal observation). The nannoplankton, which have not been studied at all, appear to be most important in terms of total metabolism (Tundisi 1969). The net plankton are usually dominated by diatoms such as *Thalassothrix* spp., *Chaetoceras* spp., *Nitzschia* spp., *Skeletonema* spp., and *Rhizosolenia* spp. (Mattox 1949; Wood 1965; Walsh 1967; Bacon 1970). At times, blooms of dinoflagellates such as *Peridinium* spp. and *Gymnodinium* spp. may dominate (personal observation). In many locations, particularly in shallow waters with some turbulence, benthic diatoms such as *Pleurosigma* spp., *Mastogloia* spp., and *Diploneis* may be numerically important in the net plankton (Wood 1965).

Understanding the mangrove-associated phytoplankton community is complicated by the constant mixing of water masses in mangrove regions. Depending upon the location, the phytoplankton may be dominated by oceanic and neritic forms, by true estuarine plankton, and by freshwater plankton. The pattern of dominance may change daily or seasonally depending upon the source of the principal water mass.

Before we can understand the importance (or lack of importance) of phytoplankton in mangrove regions, some questions must be answered. How productive are the nannoplankton? How does the daily and seasonal shift in phytoplankton dominance affect community productivity? Does the generally low standing crop of phytoplankton represent low productivity or a high grazing rate?

5.3 ASSOCIATED VASCULAR PLANTS

Four species of aquatic grasses occur on bay and creek bottoms adjacent to mangrove forests. Turtle grass, *Thalassia testudinum*, and manatee grass, *Syringodium filliforme*, are two tropical sea grasses which occur in waters with average salinities above about 20 ppt. Shoal grass, *Halodule wrightii*, is found at somewhat lower salinities and widgeongrass, *Ruppia maritima*, is a freshwater grass which can tolerate low salinities. These grasses occur throughout south Florida, often in close juxtaposition to mangroves. Zieman (in prep.) presents a thorough review of sea grasses along with comments about possible energy flow linkages with mangrove ecosystems.

There are extensive areas of mangroves in south Florida which are closely associated with marshes dominated by a variety of other salt-tolerant plants. For example, along the southwest coast between Flamingo and Naples, marshes are scattered throughout the mangrove belt and also border the mangroves on the upland side. The estuarine marshes within the mangrove swamps have been extensively described by Egler (1952), Carter et al. (1973), and Olmstead et al. (1981). They contain various salt-tolerant marsh species including: salt grass, *Distichlis spicata*, black needle rush, *Juncus roemerianus*, spike rush, *Eleocharis cellulosa*, glass wort, *Salicornia* spp., Gulf cordgrass, *Spartina spartinae*, sea purslane, *Sesuvium portulacastrum*, salt wort, *Batis maritima*, and sea ox-eye, *Borrichia frutescens*. Farther north, above Tampa on the west coast of Florida, marshes populated by smooth cordgrass, Spartina alterniflora, and black needle rush, Juncus roemerianus, become more extensive and eventually replace mangrove swamps. Even in the Everglades region, the saline marshes are comparable to mangroves in areal extent, although they tend to be some distance from open water. Studies of these marshes, including assessment of their ecological value, are almost non-existent. Certainly, they have considerable importance as habitat for small fishes which, in turn, support many of the nesting wading birds in south Florida (see section 9).

Tropical hardwood forests may occur within the mangrove zone in south Florida, particularly where old shorelines or areas of storm sedimentation have created ridges 1 m or more above MSL (mean sea level) (Olmstead et al. 1981). Similar forests or "hammocks" occur to the rear of the mangrove zone on higher ground. Typical trees in both forest types include the fan palm, Thrinax radiata, buttonwood, Conocarpus erecta, manchineel, Hippomane mancinella, and, in the past, mahogany, Swietenia mahagoni. Olmstead et al. (1981) provide a description of these communities.

Freshwater marsh plants, such as the grasses, rushes and sedges that dominate the freshwater Everglades, are not mentioned here, although they are occasionally mixed in with small mangroves that have become established well inland. See Hofstetter (1974) for a review of literature dealing with these plants.

Finally, a group of somewhat salt-tolerant herbaceous plants is found within stands of mangroves. They usually occur where slight increases in elevation exist and where sufficient light filters through the mangrove canopy. Carter et al. (1973) list the following as examples of members of the mangrove community: leather ferns, Acrostichum aureum and A. danaeifolium; spanish bayonet, Yucca aloifolia; spider lily, Hymenocallis latifolia; sea blite, Suaeda linearis; chaff flower, Alternanthera ramosissima; samphire, Philoxerus vermicularis; bloodleaf, Iresine celosia; pricklypear cactus, Opuntia stricta; marsh elder, Iva frutescens; the rubber vine, Rhabdadenia biflora; the lianas, Ipomoea tuba and Hippocratea volubilis; and a variety of bromeliads (Bromeliaceae).

Although the lists of vascular plants which occur in mangrove swamps may seem extensive, the actual number of species in any given location tends to be low compared to totally freshwater environments (see Carlton 1977). Analogous to temperate salt marshes, mangrove swamps possess too many sources of stress, particularly from tidal salt water, to have a high diversity of vascular plant species.

CHAPTER 6. COMMUNITY COMPONENTS - INVERTEBRATES

6.1 ECOLOGICAL RELATIONSHIPS

The mangrove ecosystem, with its tree canopies, masses of aerial roots, muddy substrates, and associated creeks and small embayments, offers many habitat opportunities for a wide variety of invertebrates. While there are few comparisons of species richness with other types of coastal ecosystems, mangrove swamps appear to be characterized by moderately high invertebrate species diversity. Abele (1974) compared H' (Shannon Weaver) diversity of decapod crustaceans between various littoral marine communities and found mangrove swamps in an intermediate position with more decapod species than Spartina marshes but considerably less than were associated with rocky substrate communities.

There is little doubt that the maze of prop roots and muddy substrates under intertidal mangrove trees provides habitat for a wide range of invertebrates and fishes (Figure 10) (see section 7 for the latter). The nursery value of the prop root complex for juvenile spiny lobsters, Panulirus argus, is well established (Olsen et al. 1975; Olsen and Koblic 1975; Little 1977; Witham et al. 1968). According to these researchers, the phyllosome larvae of spiny lobsters often settle among the prop roots and remain there for much of their juvenile lives. The prop roots provide protection from predators and a possible source of food in the associated populations of small invertebrates. To provide the best habitat, a section of the prop roots should extend below mean low tide. If conditions are suitable, the juveniles may remain in close association with the prop root community for as much as 2 years until they reach a carapace length of 60 to 70 mm.

In addition to its value as spiny lobster habitat, mangrove ecosystems also harbor the following invertebrates: barnacles, sponges, polychaete worms, gastropod mollusks, pelecypod mollusks, isopods, amphipods, mysids, crabs, caridean shrimp, penaeid shrimp, harpacticoid copepods, snapping shrimp, ostracods, coelenterates, nematodes, a wide variety of insects, bryozoans, and tunicates. The most obvious and dominant organisms are usually barnacles, crabs, oysters, mussels, isopods, polychaetes, gastropods and, tunicates.

A striking characteristic of most mangrove swamps is the pattern of horizontal and vertical zonation of invertebrates (Figure 9). Characteristic vertical zonation patterns are found on the prop roots (Rutzler 1969) and not so obvious horizontal distributions occur as you move back into the center of the swamp (Warner 1969). Invertebrate biomass in the red mangrove zone on the edge of the swamp may be very high, often in excess of 100 dry g/m^2 of organic matter in many locations (personal observation). In the center of the swamp, particularly where there is little flooding, biomass is usually an order of magnitude less; Golley et al. (1962) found an average of 6.4 g/m^2 of invertebrates in the center of a Puerto Rican mangrove swamp.

Mangrove-associated invertebrates can be placed in four major categories based on trophic position:

(1) direct grazers - limited to

(a) insects and the mangrove tree crab, Aratus pisonii, all of which feed on leaves in the mangrove canopy and

(b) a group of small invertebrates which graze the prop root and mud algae directly;

(2) filter feeders - largely sessile prop root invertebrates which filter phytoplankton and detritus from the water;

(3) deposit feeders - mobile invertebrates which skim detritus, algae and occasional small animals from the surface of the mud and forest floor;

(4) carnivores - highly mobile invertebrates which feed upon the three preceding groups in all locations from the tree canopy (largely insects) to the mud surface. Food sources in mangrove swamps and energy flow are discussed in section 3.6.

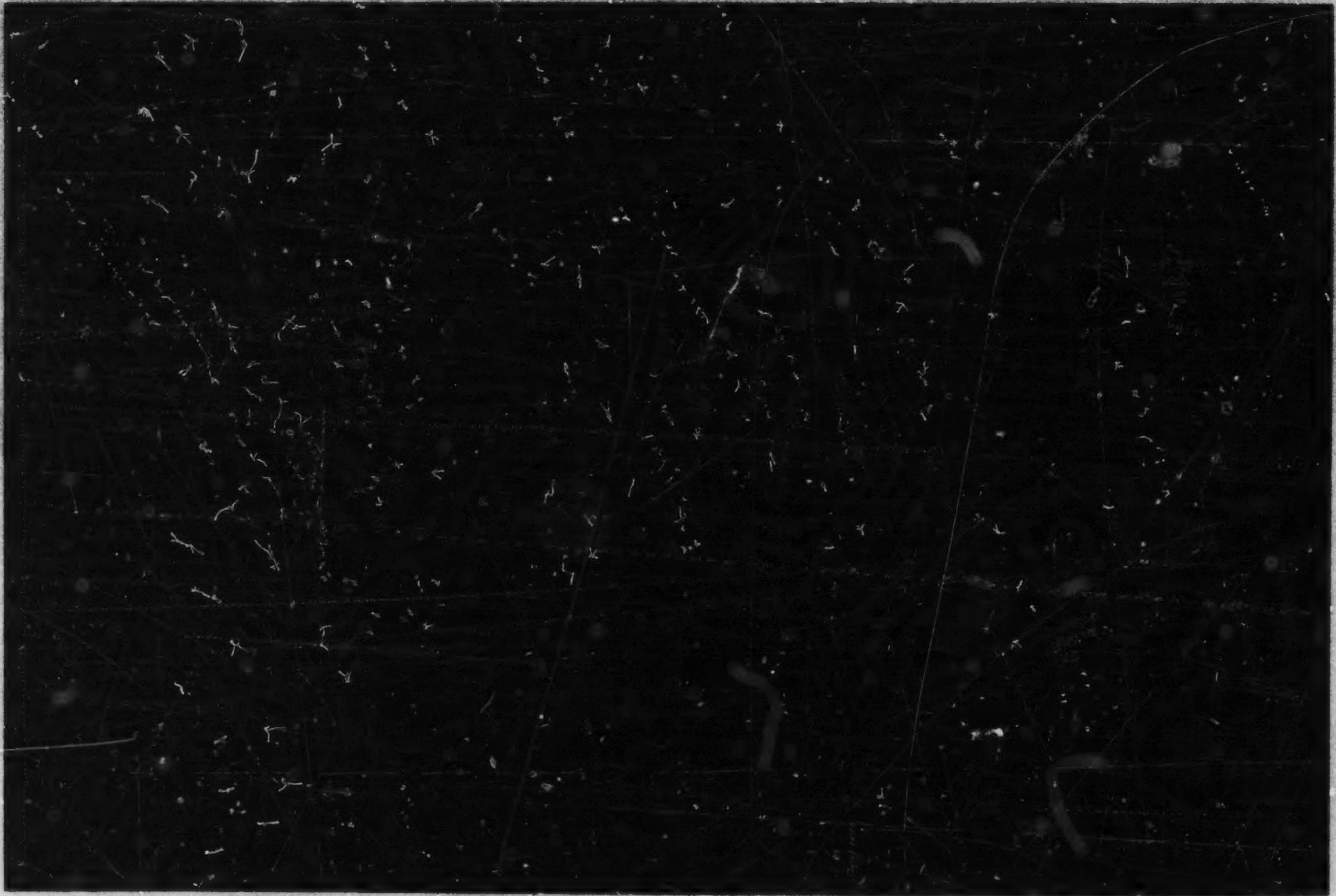


Figure 10. Photograph of red mangrove prop root habitat in clear shallow water with associated animal and plant populations. Photograph is by Bianca Lavies (copyright, National Geographic Society).

6.2. ARBOREAL ARTHROPOD COMMUNITY

A surprising variety of arthropods inhabit the mangrove canopy. Because they are frequently secretive or possess camouflage coloration, their numerical importance often has been overlooked. Beever et al. (1979) pointed out that arboreal arthropods have a variety of ecological roles: (1) direct herbivory on mangrove leaves, (2) predator-prey interactions, and (3) biomass export through frass production and leaf defoliation. Direct grazing is typically patchy in distribution. It is not unusual to find extensive stretches of mangroves that have scarcely been grazed. In nearby areas, as much as 80% of the leaves may have some damage (Beever et al. 1979). As a general rule, it is probably safe to state that healthy, unstressed mangrove stands normally have less than 10% of their total leaf area grazed (Heald 1969). In many locations, percent leaf area damaged is on the order of 1% to 2% (Beever et al. 1979). There are exceptions. Onuf et al. (1977) reported biomass loss to arthropod grazers as high as 26% in a mangrove stand where growth and nitrogen content of the leaves had been enhanced by input of nutrients from a bird rookery.

In terms of numbers of species, the dominant group of arboreal arthropods is insects. The most thorough inventory of mangrove-associated insects was conducted by Simberloff and Wilson to obtain the raw data for their papers on island biogeography (Simberloff and Wilson 1969; Simberloff 1976). These papers list over 200 species of insects associated with overwash mangrove islands in the Florida Keys. There is no reason to expect lesser numbers in other types of mangrove communities, except for the mangrove scrub forests. The most thorough study of insect grazing on mangrove leaves is that of Onuf et al. (1977) (see section 2.6).

Although not as numerically impressive as the insects, the mangrove tree crab, *Aratus pisonii*, appears to be potentially as important in terms of grazing impact (Beever et al. 1979). The life history of this secretive little crab has been described by Warner (1967). In Jamaica its numbers range from 11 to 16/m^2 at the edge of fringing swamps to 6/m^2 in the center of large swamps. Beever et al. (1979) reported typical densities for a variety of sites in south Florida of 1 to 4 crabs/m^2. These same authors reported some interesting details about the crab: (1) the diet is omnivorous ranging from fresh mangrove leaves to caterpillars, beetles, and various insects; (2) the crab suffers highest predation pressure while in the planktonic larval stage; (3) predation on the crabs while in the arboreal community is low and comes from birds such as the white ibis, raccoons, other mangrove tree crabs and, if the crabs fall in the water, fishes such as the mangrove snapper; and (4) in one location in south Florida (Pine Island Sound) they found in accordance with normal biogeographical theory, the highest densities of crabs associated with fringing forests and the lowest densities on distant islands, but at Sugar Loaf Key the unexplainable reverse distribution was found.

Other invertebrates may visit the canopy from below either for purposes of feeding or for protection from high tides. Included in this group are the pulmonate gastropods, *Littorina angulifera*, *Cerithidea scalariformis*, and *Melampus coffeus*, the isopod, *Ligea exotica*, and a host of small crabs.

In summary, with the exception of a half dozen key papers, the arboreal mangrove community has been generally ignored. Both insects and the mangrove tree crab play significant ecological roles and may affect mangrove productivity to a greater extent than has been recognized.

6.3 PROP ROOT AND ASSOCIATED MUD SURFACE COMMUNITY

These two somewhat distinct communities have been lumped together because of the large number of mobile organisms which move back and forth between tidal cycles. The aerial roots are used as protective habitat and to some extent for feeding while the nearby mud substrates are used principally for feeding.

The prop roots support an abundance of sessile organisms. The vertical zonation of both mobile and sessile invertebrates has been studied extensively in other parts of the world (Goodbody 1961; Macnae 1968; Rutzler 1969; Coomans 1969; Bacon 1970; Kolehmainen 1973; Sasekumar 1974; Yoshioka 1975). Vertical zonation certainly exists on Florida red mangrove roots. The generalized scheme shown in Figure 9 essentially contains two zones: an upper zone dominanted by barnacles and a lower zone dominated by mussels, oysters and ascidians. Between mean high tide and mean tide, the wood boring isopod, *Sphaeroma terebrans* (discussed at length in section 2.7) is important, both numerically and through the provision of numerous holes for use by other organisms (Estevez 1978).

The most complete study of the Florida mangrove prop root community is Courtney's (1975) comparison of seawall and mangrove associations. He reported an extensive list of invertebrates from mangrove prop roots at Marco Island, Florida, including: *Crassostrea virginica*, *Littorina angulifera*, *Crepidula plana*, *Diodora cayenensis*, *Urosalpinx perrugata*, *Pisania tincta*, *Brachidontes exustus*, nine species of polychaetes, *Sphaeroma terebrans*, *Palaemon floridanus*, *Periclimenes longicaudatus*, *Synalpheus fritzmuelleri*, *Thor floridanus*, *Petrolisthes armatus*, and at least eight species of crabs. The following species were found only on mangrove roots and not on seawalls: *Turitella* sp., *Melongena corona*, *Anachis semiplicata*, *Bulla striata*, *Hypselodoris* sp., *Arca imbricata*, *Carditamera floridana*, *Pseudoirus typica*, and *Martesia striata*.

Tabb et al. (1962) and Odum and Heald (1972) reported a variety of invertebrates associated with prop roots in the Whitewater Bay region. Although many species coincide with Courtney's (1975) list, there are also significant differences due to the lower salinities in this region. It is probably safe to conclude that prop root communities vary somewhat from site to site in response to a number of factors including latitude, salinity, and proximity to other communities such as sea grass beds and coral reefs.

Sutherland (1980), working on red mangrove prop root communities in Venezuela, found little change in the invertebrate species composition on individual prop roots during an 18-month period. The species composition varied greatly, however, between adjacent prop roots, presumably in response to stochastic (chance) processes.

The mud flats adjacent to mangroves provide feeding areas for a range of invertebrates that scuttle, crawl, and swim out from the cover of the mangrove roots. Some emerge at low tide and feed on algae, detritus, and small invertebrates on the mud flats while they are high and dry. Others emerge while the tide is in, particularly at night, and forage across the flooded flats in search of the same foods plus other invertebrates which have emerged from the mud. In many ways the mangrove-mud flat relationship is analogous to the coral reef (refuge) sea grass (feeding area) relationship reviewed by Zieman (in prep.). The net effect is that the impact of the mangrove community may extend some distance beyond the boundaries of the mangrove forest.

In addition to the organisms which move from the mangroves to the mud flats, there is a small group which uses the substrate adjacent to mangroves for both habitat and feeding. In the Whitewater Bay region, four crabs exploit the intertidal muds from the safety of burrows: *Uca pugilator*, *U. speciosa*, *U. thayeri*, and *Eurytium limosum* (Tabb et al. 1962). In low salinity mangrove forests of south Florida, the crayfish, *Procambarus alleni*, is a dominant member of the burrowing, benthic community (Hobbs 1942) as is the crab, *Rhithropanopeus harrisii* (Odum and Heald 1972). Both organisms are found in a remarkable number of fish stomachs.

The benthic fauna and infauna of creek and bay bottoms near mangrove forests are highly variable from one location to the next. Many of these organisms, particularly the deposit and filter feeders, benefit from particulate organic matter originating from mangrove litter fall (Odum and Heald 1972, 1975b). Tabb and Manning (1961) and Tabb et al. (1962) present lists and discussions of many of the benthic invertebrates adjacent to mangrove areas of Whitewater Bay. Weinstein et al. (1977) compared the benthic fauna of a mangrove-lined creek and a nearby man-made canal on Marco Island. They found (1) the mangrove fauna to be more diverse than the canal fauna and (2) a higher diversity of organisms at the mouths of mangrove creeks than in the "heads" or upstream ends. Courtney (1975) found the same pattern of upstream decreases in diversity, presumably in response to decreasing oxygen concentrations and increasingly finer sediments.

Finally, the irregularly flooded substrates in the center of mangrove forests contain a small but interesting assemblage of invertebrates. The litter layer, composed largely of mangrove leaves, evidently includes a variety of nematodes. Due to the usual taxonomic difficulties in identifying nematodes, complete species lists do not exist for mangrove forests; however, many species and individuals are associated with the decaying leaves (Hopper et al. 1973). In addition to nematodes, the wetter sections of the swamp floor can contain mosquito and other insect larvae, polychaetes, harpacticoid copepods, isopods, and amphipods. Simberloff (1976) lists 16 species of insects associated with the muddy floor of mangrove forests. Roaming across the forest floor during low tide are several crustaceans including the mangrove tree crab, *Aratus pisonii*, crabs of the genus *Sesarma*, and the pulmonate gastropods, *Melampus coeffeus* and *Cerithidea scalariformis*. Both snails clearly have the ability to graze and consume recently fallen leaves (personal observation). With favorable conditions (relatively frequent tidal inundation plus the presence of red mangroves) *Melampus* populations can exceed 500/m^2 and average 100 to 200/m^2 (Heald, unpublished data). *Cerithidea* is found largely in association with black mangroves and can reach densities of at least 400/m^2.

6.4 WATER COLUMN COMMUNITY

This section is embarrassingly short; the reasons for this brevity are (1) the paucity of research on zooplankton in Florida mangrove-dominated areas and (2) our inability to discover some of the work which undoubtedly has been done. Davis and Williams (1950) are usually quoted as the primary reference on Florida mangrove-associated zooplankton, but their paper only lists zooplankters collected in two areas. Zooplankton near mangroves are probably no different from those found in other shallow, inshore areas in south Florida. Based on Davis and Williams (1950) and Reeve (1964), we can hypothesize that the community is dominated by copepod species of genus *Acartia*, particularly *Acartia tonsa*. In addition, we could expect a few other calanoid copepods, arrow worms (*Sagitta* spp.), many fish, polychaete and crustacean larvae and eggs. Another component of the "plankton," particularly at night, are benthic amphipods, mysids, and isopods which leave the bottom to feed (personal observation).

Plankton are not the only invertebrates in the water column. Swimming crabs, such as the blue crab, *Callinectes sapidus*, are plentiful in most estuarine mangrove regions of south Florida. Other swimming crustaceans include the caridean shrimp (*Palaemonetes* spp. and *Periclimenes* spp.), the snapping shrimp (*Alpheus* spp.), and the penaeid shrimp (*Penaeus* spp). All of these swimming crustaceans spend considerable time on or in the benthos and around mangrove prop roots. From the economic point of view, the pink shrimp, *Penaeus duorarum*, is probably the most important species associated with mangrove areas (see discussion in section 11).

CHAPTER 7. COMMUNITY COMPONENTS - FISHES

Of the six mangrove community types discussed in section 1.5, fishes are an important component of four: (1) basin forests, (2) riverine forests, (3) fringe forests, and (4) overwash island forests. For convenience we have divided fringe forests into two sub-components: (a) forests which fringe estuarine bays and lagoons and (b) forests which fringe oceanic bays and lagoons. This division is necessary because the fish communities differ markedly.

Mangroves serve two distinct roles for fishes and it is conceptually important to distinguish between them. First, the mangrove-water interface, generally red mangrove prop roots, afford a relatively protected habitat which is particularly suitable for juvenile fishes. Secondly, mangrove leaves, as discussed in section 3.6, are the basic energy source of a detritus-based food web on which many fishes are dependent. The habitat value of mangroves can be considered strictly a function of the area of interface between the water and the mangrove prop roots; it is an attribute shared by all four types of mangrove communities. The importance of the mangrove detritus-based food web is dependent on the relative contribution of other forms of energy in a given environment, including phytoplankton, benthic algae, sea grass detritus, and terrestrial carbon sources. Figure 11 provides a diagrammatic representation of the relative positions along a food web continuum of the four mangrove communities.

Fishes recorded from mangrove habitats in south Florida are listed in Appendix B. Although the fish communities are discussed separately below, they have been combined into certain categories in Appendix B; fishes from mangrove basins and riverine forests have been combined under the heading of tidal streams; fishes from fringing forests along estuarine bays and lagoons are listed under the heading of estuarine bays; fishes from oceanic bays and lagoons have been listed under oceanic bays. Since no surveys have been published specifically relating to overwash island forests, there is no listing for this community type in Appendix B. Site characteristics and sampling methods for these community types are summarized in Appendix A. Nomenclature and taxonomic order follow Bailey et al. (1970).

7.1 BASIN MANGROVE FORESTS

The infrequently flooded pools in the black mangrove-dominated zone provide an extreme habitat which few species of fishes can tolerate. The waters are darkly stained with organic acids and tannins leached from the thick layer of leaf litter. Dissolved oxygen is frequently low (1-2 ppm) and hydrogen sulfide is released from the sediments following physical disturbance. Salinities are highly variable ranging from totally fresh to hypersaline. The fish families best adapted to this habitat are the euryhaline cyprinodonts (killifishes) and the poeciliids (livebearers). The killifishes include *Fundulus confluentus* (Heald et al. 1974), *Rivulus marmoratus* (M. P. Weinstein, Va. Commonwealth Univ., Richmond, Va.; personal communication 1981), *Floridichthys carpio*, and *Cyprinodon variegatus* (Odum 1970). The poeciliids include *Poecilia latipinna* (Odum 1970) and, the most common, *Gambusia affinis* (Heald et al. 1974). While the species richness of fishes in this habitat is low, the densities of fish are often very high. Weinstein (pers. comm.) has recorded up to 38 fish/m^2.

All of these fishes are permanent residents, completing their life cycles in this habitat. They feed primarily on mosquito larvae and small crustaceans such as amphipods which, in turn, feed on mangrove detritus and algae. These small fishes enter coastal food webs when they are flushed into the main watercourses during high spring tides or following seasonally heavy rains. Here they are eaten by numerous piscivorous fishes including snook, ladyfish, tarpon, gars, and mangrove snappers. The alternate energy pathway for fishes of the black mangrove basin wetlands occurs when the pools shrink during dry weather, the fishes are concentrated into smaller areas, and are fed-upon by various wading birds including

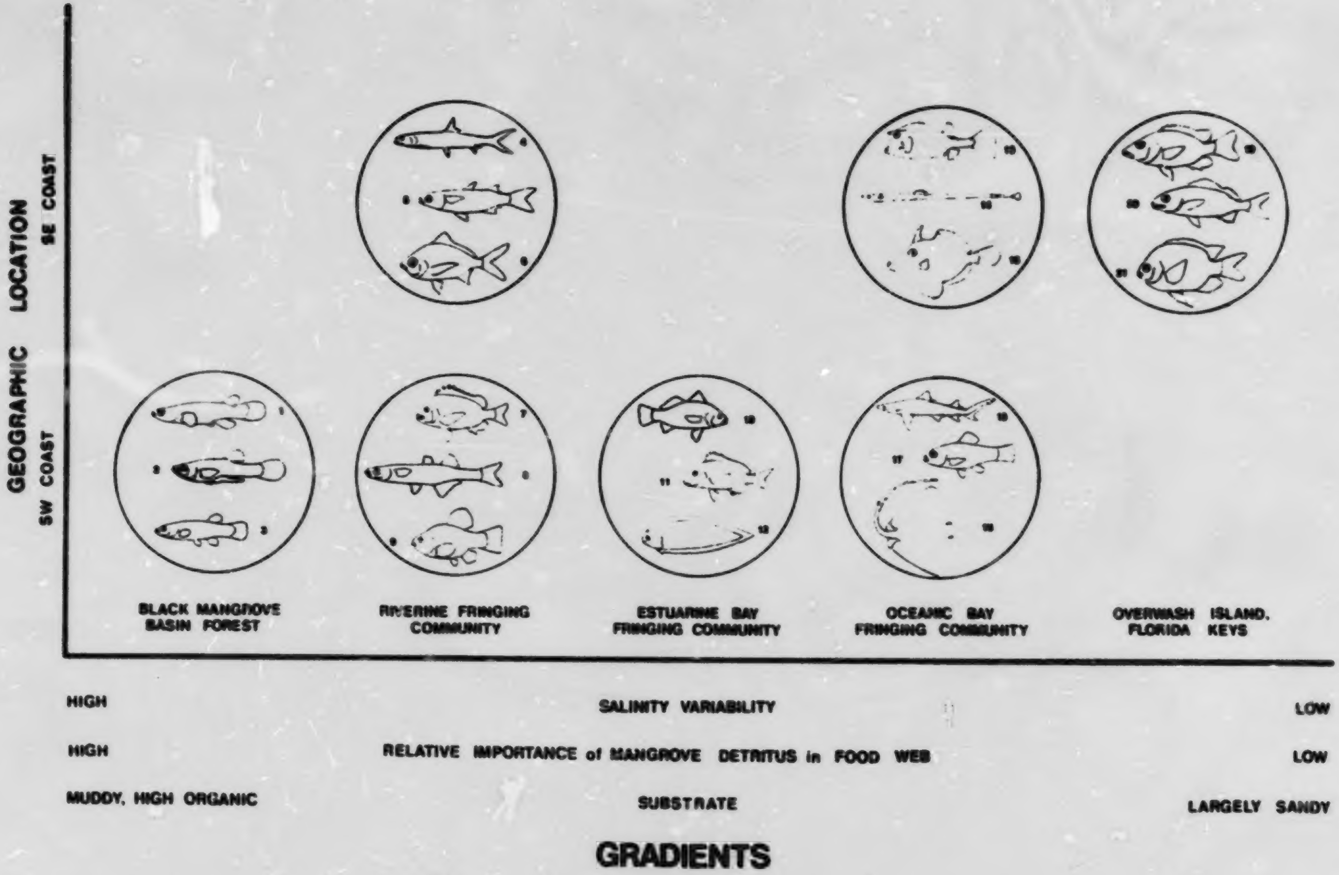

GEOGRAPHIC LOCATION
SE COAST
SW COAST
BLACK MANGROVE BASIN FOREST
RIVERINE FRINGING COMMUNITY
ESTUARINE BAY FRINGING COMMUNITY
OCEANIC BAY FRINGING COMMUNITY
OVERWASH ISLAND, FLORIDA KEYS
HIGH
SALINITY VARIABILITY
LOW
HIGH
RELATIVE IMPORTANCE of MANGROVE DETRITUS in FOOD WEB
LOW
MUDDY, HIGH ORGANIC
SUBSTRATE
LARGELY SANDY
GRADIENTS

Figure 11. Gradient of mangrove-associated fish communities showing representative species. Fish are not drawn to scale. 1 = rivulus, 2 = mosquitofish, 3 = marsh killifish, 4 = ladyfish, 5 = striped mullet, 6 = yellowfin mojarra, 7 = juvenile sheepshead, 8 = tidewater silversides, 9 = sheepshead minnow, 10 = silver perch, 11 = pigfish, 12 = blackcheek tonguefish, 13 = scrawled cowfish, 14 = fringed pipefish, 15 = fringed filefish, 16 = lemon shark, 17 = goldspotted killifish, 18 = southern stingray, 19 = juvenile schoolmaster, 20 = juvenile tomtate, 21 = juvenile sergent major. See Appendix B for scientific names.

herons, ibis and the wood stork (Heald et al. 1974).

7.2 RIVERINE FORESTS

Tidal streams and rivers, fringed largely by red mangroves, connect the freshwater marshes of south Florida with the shallow estuarine bays and lagoons (Figure 12). Few of these streams have been studied thoroughly. The exception is the North River which flows into Whitewater Bay and was studied by Tabb (1966) and Odum (1970). Springer and Woodburn (1960) collected fishes in a bayou or tidal pass connecting Boca Ciega Bay and Old Tampa Bay. Carter et al. (1973) reported on the fishes of two tidal streams entering Fahkahatchee and Fahka Union Bays. Nugent (1970) sampled fishes in two streams on the western shore of Biscayne Bay. Characteristics of these areas and sampling gear used by the investigators are summarized in Appendix A.

These tidal streams and associated riverine mangrove forests exhibit extreme seasonal variability in both physical characteristics and fish community composition. Salinity variations are directly related to changes in the make-up of the fish assemblage. During the wet season (June - November), salinities fall throughout the water courses and, at some locations in certain heavy runoff years, become fresh all of the way to the mouth (Odum 1970). Opportunistic freshwater species, which are normally restricted to the sawgrass and black needle rush marshes of the headwaters, invade the mangrove zone. These include the Florida gar, *Lepisosteus platyrhincus*; several centrarchid sunfishes of the genus *Lepomis* and the largemouth bass, *Micropterus salmoides*; the freshwater catfishes, *Ictalurus natalis* and *Noturus gyrinus*; and the killifishes normally considered freshwater inhabitants such as *Lucania goodei* and *Rivulus marmoratus*.

During the dry season (December to early May) salinities rise as a result of decreased freshwater runoff and continuing evaporation. Marine species invade the tidal streams primarily on feeding forays. Examples include the jewfish, *Epinephelus itajara*, the stingrays (Dasyatidae), the needlefishes (Belonidae), the jacks (Carangidae), and the barracuda, *Sphyraena barracuda*. Other seasonal movements of fishes appear to be temperature related. Tabb and Manning (1961) documented movements of a number of species from shallow inshore waters to deeper water during times of low temperature stress. The lined sole, the hogchoker, the bighead searobin, and the striped mullet, for example, are much less frequently caught in winter in shallow inshore waters.

A third type of seasonality of fish populations in the tidal rivers is related to life cycles. Many of the fish which utilize the tidal stream habitat do so only as juveniles. Thus, there are peaks of abundance of these species following offshore spawning when larval or juvenile forms are recruited to the mangrove stream habitat. In general, recruitment occurs in the late spring or early summer following late winter and spring spawning offshore or in tidal passes (Reid 1954). Numerous species are involved in this life cycle phenomenon including striped mullet, grey snapper, sheepshead, spotted sea trout, red drum, and silver perch.

The only estimate of fish standing crop from tidal stream habitats is that of Carter et al. (1973). They recorded 27 species weighing 65,891 g (wet wt.) from an area of 734 m^2 or about 90 g/m^2. This is probably an overestimate since an unknown portion of the fish community had moved from the flooded lowlands to the stream on the ebb tide; sampling occurred at low tide in October. Nonetheless, this is an indication of the high fish standing crop which this mangrove-associated habitat can support. The number of species reported from individual tidal streams annually ranges from 47 to 60 and the total from all tidal streams in southwest Florida is 111 species (Appendix B).

The food webs in these riverine mangrove ecosystems appear to be predominantly mangrove detritus-based, although the Biscayne Bay stream studied by Nugent

Figure 12. Aerial photograph of the mangrove belt of southwest Florida near Whitewater Bay. Note the complex system of pools and small creeks which connect with the tidal river system.

(1970) may be an exception. The basic link between the mangrove leaf and higher order consumers is provided by microorganisms (fungi, bacteria, Protozoa) which colonize the decaying leaf and convert them into a relatively rich protein source (Odum 1970; Odum and Heald 1975a). These decaying leaf fragments with associated microorganisms are fed upon by a group of omnivorous detritivores including amphipods, mysids, cumaceans, ostracods, chironomid larvae, harpacticoid and calanoid copepods, snapping shrimp, caridean and penaeid shrimp, a variety of crabs, filter-feeding bivalves and a few species of fishes (Odum 1970; Odum and Heald 1972; Odum and Heald 1975b). These detritivores, in turn, are consumed by a number of small carnivorous fishes, which in turn, are consumed by larger piscivorous fishes. The concept of mangrove trophic structure is also discussed in section 3.6. See Appendix B for species specific dietary information.

The tidal creeks studied by Nugent (1970) on the western shore of Biscayne Bay differ from the previously discussed streams in the Everglades estuary. The mouths of the Biscayne Bay creeks have dense growths of sea grasses which contribute sea grass detritus. The salinities are considerably greater and the streams are located only a few kilometers from coral reefs, which are largely absent on Florida's west coast, at least close to shore. As a result, 23 species listed in Appendix B were captured by Nugent (1970) and are not recorded from riverine mangrove habitat on the west coast of Florida. Examples include several of the grunts (Pomadasyidae), the gray triggerfish, *Balistes capriscus*, the barbfish, *Scorpaena brasiliensis*, the scrawled boxfish, *Lactophrys quadricornis*, and the snappers, *Lutjanus apodus* and *L. synagris*.

Riverine mangrove communities and associated tidal streams and rivers are typified by the following families of fishes: killifishes (Cyprinodontidae), livebearers (Poeciliidae), silversides (Atherinidae), mojarras (Gerreidae), tarpon (Elopidae), snook (Centropomidae), snappers (Lutjanidae), sea catfishes (Ariidae), gobies (Gobiidae), porgys (Sparidae), mullets (Mugilidae), drums (Sciaenidae), and anchovies (Engraulidae). The mangrove-lined streams and associated pools are important nursery areas for several marine and estuarine species of gamefish. The tarpon, *Megalops atlantica*, snook, *Centropomus undecimalis*, and ladyfish, *Elops saurus*, utilize these areas from the time they reach the estuary as post-larvae, having been spawned offshore. Gray snapper, *Lutjanus griseus*, sheepshead, *Archosargus probatocephalus*, spotted seatrout, *Cynoscion nebulosus*, and red drum, *Sciaenops ocellata*, are recruited to grass beds of shallow bays and lagoons as post-larvae and enter the mangrove-lined streams for the next several years (Heald and Odum 1970). Of these species, only the spotted seatrout probably spawns in the estuary (Tabb 1966). Other species of commercial or game importance which use the riverine fringing habitat include crevalle jack, gafftopsail catfish, jewfish, striped mojarra, barracuda, Atlantic thread herring, and yellowfin menhaden (Odum 1970).

7.3 FRINGING FORESTS ALONG ESTUARINE BAYS AND LAGOONS

Mangrove-fringed estuarine bays and lagoons are exemplified by the Ten Thousand Islands area and Whitewater Bay. Quantitative fish data are available from Fahkahatchee Bay (Carter et al. 1973; Yokel 1975b; Seaman et al. 1973), Fahka Union Bay (Carter et al. 1973), Rookery Bay (Yokel 1975a), the Marco Island Estuary (Weinstein et al. 1977; Yokel 1975a), and Whitewater Bay (Clark 1970). Individual site characteristics are summarized in Appendix A. All except Fahka Union Bay contain significant amounts of sea grasses. Macroalgae dominate the benthic producers of Fahka Union Bay. Studies by Reid (1954) and Kilby (1955) near Cedar Key, Florida, were not included in our summary because mangroves are sparse in this area and no mention of mangrove collecting sites were made by these authors. Studies of Caloosahatchee Bay (Gunter and Hall 1965) and of Charlotte Harbor (Wang and Raney 1971) were omitted because the areas studied have been highly modified and because data from many habitats were pooled in the final presentation.

All of the bays reviewed in our summaries are fringed by dense growths of red mangroves and all contain small mangrove islets. Carter et al. (1973), in their studies of Fahkahatchee and Fahka Union bays, estimated that 57% to 80% of the total energy budget of these two bays is supported by exports of particulate and dissolved organic matter from the mangroves within the bays and inflowing tidal streams. Lugo et al. (1980) estimated that the mangroves surrounding Rookery Bay provide 32% of the energy base of the heterotrophic community found in the bay.

Salinities in these bays tend to be higher than in the tidal streams and rivers and the fish assemblages reflect both this feature and the added habitat dimension of sea grass and macro algae beds. Truly freshwater species are rare in these communities and a proportionally greater percentage of marine visitors is present. The dominant fish families of the benthic habitat include drums (Sciaenidae), porgys (Sparidae), grunts (Pomadasyidae), mojarras (Gerreidae), snappers (Lutjanidae), and mullet (Mugilidae). Other familes with sizeable contributions to the benthic fauna include pipefishes (Syngnathidae), flounder (Bothidae), sole (Soleidae), searobins (Triglidae), and toadfishes (Batrachoididae).

Numerically abundant fishes of the mid and upper waters include anchovies (Engraulidae), herrings (Clupeidae) and needlefishes (Belonidae). At all locations studied, the benthic fauna was dominated by the pinfish, Lagodon rhomboides, the silver perch, Bairdiella chrysura, the pigfish, Orthopristis chrysoptera, and the mojarras, Eucinostomus gula and E. argenteus. The most common midwater and surface species include the two anchovies, Anchoa mitchilli and A. hepsetus, and two clupeids, Brevoortia smithi and Harengula pensacolae. The total number of species recorded in the individual studies ranged from 47 to 89; a total of 117 species was collected in these mangrove-fringed bays and lagoons (Appendix B).

In none of these studies were the fishes specifically utilizing the fringing mangrove habitat enumerated separately from those collected in the bay as a whole. The collections were most often at open water stations easily sampled by otter trawl. Carter et al. (1973) had two shore seine stations adjacent to mangroves but the data were pooled for publication. Of the four stations in Rookery Bay sampled by Yokel (1975a), one was immediately adjacent to the fringing mangrove shoreline and had moderate amounts of sea grasses.

The typical pattern which emerges from many estuarine studies is that relatively few fish species numerically dominate the catch. This is certainly true in mangrove-fringed estuaries. In Rookery Bay (Yokel 1975a) six species comprised 88% of the trawl-catchable fishes, in Fahkahatchee Bay seven species comprised 97% of the catch from three capture techniques (Carter et al. 1973), and in the Marco Island estuary 25 species comprised 97% of the trawl-catchable fishes (Weinstein et al. 1977).

Like tidal river and stream communities, these shallow bays serve as nurseries for numerous species of estuarine-dependent fishes that are spawned offshore. Based on the distribution and abundance of juvenile fishes of all species in six habitats, Carter et al. (1973) ranked the mangrove-fringed bays as the most important nursery grounds; the tidal streams were a close second. Shallow bays and tidal streams provide safe nurseries due to seasonally abundant food resources and the low frequency of large predators (Carter et al. 1973; Thayer et al. 1978). The relative lack of large predaceous fishes is probably due to their general inability to osmoregulate in waters of low and/or fluctuating salinity.

As in tidal streams, the peak abundance of juvenile and larval fishes in the bays is in spring and early summer (Reid 1954). In general, the highest standing crops and the greatest species richness of fishes occur in the late summer and early fall (Clark 1970). Fish densities decline in the autumn and winter as many fishes move to deeper waters.

7.4 FRINGING FORESTS ALONG OCEANIC BAYS AND LAGOONS

Mangrove-fringed "oceanic" bays and lagoons are exemplified by Porpoise Lake in eastern Florida Bay (Hudson et al. 1970), western Florida Bay (Schmidt 1979), southern Biscayne Bay (Bader and Roessler 1971), and Old Rhodes Key Lagoon in eastern Biscayne Bay (Holm 1977). Characteristics of these sites are summarized in Appendix A. Compared to the mangrove-fringed bays discussed in the previous section, these environments generally exhibit clearer water, sandier substrates, and higher and less variable salinities. Closer proximity to the Florida reef tract, the Atlantic Ocean, and the Gulf of Mexico results in a larger potential pool of fish species. These four locations have produced reports of 156 fish species (Appendix B).

Mangrove fringes make up a relatively small proportion of these environments; accordingly, their contribution to the bay food webs is probably not very large. Bader and Roessler (1972) estimated that the fringing mangrove community contributes approximately 1% of the total energy budget of southern Biscayne Bay; they considered only mainland mangroves and did not include the small area of mangrove islands. The main ecological role of the fringing mangroves in this type of environment is probably twofold. First, they increase the habitat diversity within an otherwise relatively homogeneous bay system. Second, they provide a relatively protected habitat for juvenile fishes (and certain invertebrates) that later move to more open water or coral reef communities. The second role is analogous to one of the ecological roles of sea grass communities (see Zieman, in prep.) although the fish species involved may be different.

Based primarily on habitat designations of Voss et al. (1969), the fishes of Biscayne Bay can be characterized as to preferred habitat. Of the three main habitat types, (1) rock/coral/seawall, (2) grassbed/tidal flat, and (3) mangrove, the grassbed/tidal flat ranked first in fish species occurrences. One hundred and twenty-two of 156 species (79%) are known to occur in this environment. Rock/coral/seawall habitats were frequented by 49 species (32%) and mangroves are known to be utilized by 54 species (35%) of the total fish species recorded from this bay.

7.5 OVERWASH MANGROVE ISLANDS

In terms of fish-related research, these communities are the least studied of all mangrove community types in south Florida. They are typified by the low-lying mangrove-covered islands that occur in the Florida Keys and Florida Bay and may be overwashed periodically by the tides. Examples include Shell Key, Cotton Key, and the Cowpens. Islands of this type extend southwest from the Florida mainland through the Marquesas. The Dry Tortugas lack well-developed mangrove communities although stunted trees are found (Davis 1942).

These islands are the most oceanic of any of the mangrove communities discussed. They are characterized by relatively clear water (Gore 1977) and are largely free of the freshwater inflow and salinity variations which characterize other Florida mangrove communities to varying degrees. Numerous statements exist in the literature acknowledging the frequent proximity of mangrove islands to coral reefs and sea grass beds (McCoy and Heck 1976; Thayer et al. 1978). Olsen et al. (1973) working in the U.S. Virgin Islands, found 74% to 93% overlap in the fish species composition of fringing coral reefs and shallow mangrove-fringed oceanic bays. Voss et al. (1969) listed fish species that were collected from all three types of communities: fringing mangroves, coral reefs and sea grass beds in Biscayne Bay, but there appears to have been no systematic survey of the fish assemblage characteristic of the mangrove-covered or mangrove-fringed Florida Keys. No one has quantified the faunal connections which we hypothesize exist between the mangroves and sea grasses and between the mangroves and coral reefs.

In the absence of published data from the mangrove key communities, only tentative statements can be made. In general, we expect that while mangrove islands serve as a nursery area for juvenile fishes, this function is limited largely to coral reef and marine inshore fishes and not the estuarine-dependent species that we have discussed previously. The latter (juvenile snook, red drum, spotted seatrout) appear to require relatively low salinities not found in association with most of the overwash islands. Casual observation around the edges of these islands suggests that characteristic fishes include the sea bass family (Serranidae), triggerfishes (Balistidae), snappers (Lutjanidae), grunts (Pomadasyidae), porgies (Sparidae), parrotfishes (Scaridae), wrasses (Labridae), bonefishes (Albulidae), jacks (Carangidae), damselfishes (Pomacentridae), and surgeonfishes (Acanthuridae); many of these fishes occur on or are associated with coral reefs. We also suspect that considerable overlap occurs in the fish assemblage of these mangrove islands and sea grass communities; examples include puffers (Tetraodontidae), pipefishes (Syngnathidae), gobies (Gobiidae) and scorpionfishes (Scorpaenidae). Stark and Schroeder (1971) suggested that juvenile gray snapper, which use the fringing mangroves of the keys as shelter during the day, forage in adjacent sea grass beds at night. In the absence of salinity barriers, predatory fishes probably enter the fringes of these mangrove islands on the rising tide. Included in this group are sharks, tarpon, jacks, snook, bonefish and barracuda.

7.6 GRADIENT OF MANGROVE COMMUNITY INTERACTIONS

Mangrove communities occur under a wide range of conditions from virtually freshwater at the headwaters of tidal streams to nearly oceanic conditions in the Florida Keys. Attempting to present a single list of fish characteristic of mangrove environments (Appendix B) can be misleading. For this reason we presented the concept of a continuum or complex gradient in Figure 11 and have followed that scheme throughout section 7. The gradient stretches from seasonally fresh to oceanic conditions, from highly variable salinities to nearly constant salinity, from muddy and limestone substrates to sandy substrates, from dark-stained and sometimes turbid waters to clear waters, and from food webs that are predominantly mangrove detritus-based to food webs based primarily on other energy sources. Clearly, there are other gradients as one moves from north to south in the State of Florida. At the northern end of the State, temperatures are more variable and seasonally lower than in the south. Sediments change from predominantly silicious in central and north Florida to predominantly carbonate in extreme south Florida. Nevertheless, the complex gradient shown in Figure 11, while greatly simplified for graphic purposes, suggests that characteristic fish assemblages replace one another along a gradient of changing physical and biogeographic conditions. Such a concept is useful in understanding the factors controlling the composition of fish assemblages associated with mangroves of the four major community types in south Florida.

CHAPTER 8. COMMUNITY COMPONENTS - AMPHIBIANS AND REPTILES

Food habits and status of 24 species of turtles, snakes, lizards, and frogs of the Florida mangrove region are given in Appendix C. Any of three criteria had to be met before a species was included in this table: (1) a direct reference in the literature to mangrove use by the species, (2) reference to a species as being present at a particular geographical location within the mangrove zone of Florida, and (3) North American species recorded from mangroves in the West Indies or South America, but not from Florida. This last criterion assumes that a species which can utilize mangroves outside of Florida will be able to use them in Florida. Ten turtles are listed of which four (striped mud turtle, chicken turtle, Florida red-bellied turtle, and softshell turtle) are typical of freshwater. Two (mud turtle and the ornate diamondback terrapin) are found in brackish water and the remainder (hawksbill, green, loggerhead, and Atlantic ridley) are found in marine waters.

Freshwater species usually occur in the headwater regions of mangrove-lined river systems. All four freshwater species are found in habitats other than mangrove swamps including streams, ponds, and freshwater marshes. The brackish water species are found in salt marshes in addition to mangrove swamps. Mangroves, however, are the principal habitat for the ornate diamondback terrapin (Ernst and Barbour 1972). Carr and Goin (1955) listed two subspecies of the diamondback: Malaclemys terrapin macrospilota and M. t. rhizophorarum. Malaclemys terrapin macrospilota inhabits the southwest and southern coasts, and M. t. rhizophorarum is found in the Florida Keys. The two subspecies intergrade in the region of northern Florida Bay.

All four of the marine turtles are associated with mangrove vegetation at some stage of their lives. Loggerhead and green turtles are apparently much less dependent on mangroves than the remaining two, although we strongly suspect that recently hatched loggerheads may use mangrove estuaries as nursery areas. Green turtles are generally believed to feed on a variety of submerged aquatic plants and sea grasses; recent evidence has shown that they also feed on mangrove roots and leaves (Ernst and Barbour 1972). The Atlantic ridley's preferred habitat is "shallow coastal waters, especially the mangrove-bordered bays of the southern half of the peninsula of Florida" (Carr and Goin 1955). Hawksbill turtles feed on a variety of plant materials including mangrove (especially red mangrove), fruits, leaves, wood, and bark (Ernst and Barbour 1972).

Three species in the genus Anolis have been reported from Florida mangroves: the green anole, the cuban brown anole, and the Bahaman bank anole. All are arboreal lizards that feed on insects. The green anole is widespread throughout the Southeastern United States and is not at all dependent on mangrove swamps. The other two species have much more restricted distributions in the United States and are found only in south Florida. They also are not restricted to mangrove ecosystems. Of the six species of snakes listed, the mangrove water snake (Figure 13) is most dependent upon mangrove habitats.

Two important species of reptiles found in mangrove swamps are the American alligator and the American crocodile. The alligator is widespread throughout the Southeastern United States and is only incidentally found in low salinity sections of Florida mangrove areas (Kushlan 1980). The American crocodile is rare; historically its distribution was centered in the mangrove-dominated areas of the upper and lower Florida Keys (particularly Key Largo) and the mangrove-lined shorelines and mud flats along the northern edge of Florida and Whitewater Bays (Kushlan 1980). Mangroves appear to be critical habitat for this species. Its range has shrunk considerably in south Florida since the 1930's, even though Florida Bay was added to Everglades National Park in 1950 (Moore 1953; Ogden 1978). Much of the decrease in range is due to increased human activity in the Florida Keys. The remaining population centers of the American crocodile are in

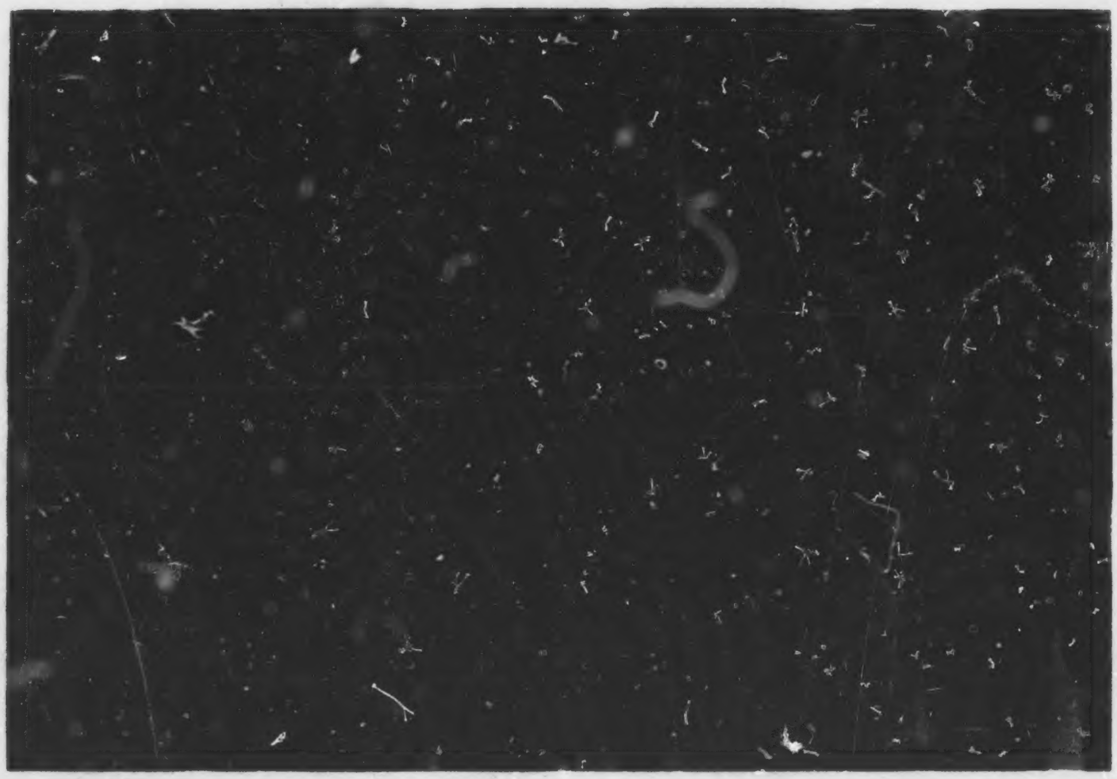


Figure 13. The mangrove water snake, Nerodia fasciata compressicauda, curled on a red mangrove prop root. Photograph by David Scott.

northern Florida Bay and adjacent coastal swamps and the northern end of Key Largo (Ogden 1978; Kushlan 1980). The species uses a variety of habitats for nesting in the Florida Bay region including open hardwood thickets along creek banks, hardwood-shrub thickets at the heads of sand-shell beaches, and thickets of black mangroves behind marl banks (Ogden 1978). On Key Largo the crocodile locates its nests on creek and canal banks in red and black mangrove swamps (Ogden 1978). Mangrove areas thus appear to be important in the breeding biology of this endangered species.

Interestingly, only three species of amphibians, to our knowledge, have been recorded in Florida mangrove swamps (Appendix C). This is due to two factors: (1) lack of detailed surveys in low salinity swamps and (2) the inability of most amphibians to osmoregulate in salt water. No doubt, several additional species occur in the freshwater-dominated hammock and basin mangrove communities inland from the coast. Possible additional species include: the eastern narrow-mouthed toad, *Gastrophryne carolinensis*, the eastern spadefoot toad, *Scaphiopus holbrooki*, the cricket frog, *Acris gryllus*, the green tree frog, *Hyla cinerea*, and the southern leopard frog, *Rana utricularia*.

CHAPTER 9. COMMUNITY COMPONENTS - BIRDS

9.1 ECOLOGICAL RELATIONSHIPS

Because mangroves present a more diverse structural habitat than most coastal ecosystems, they should harbor a greater variety of birdlife than areas such as salt marshes, mud flats, and beaches (MacArthur and MacArthur 1961). The shallow water and exposed sediments below mangroves are available for probing shorebirds. Longer-legged wading birds utilize these shallow areas as well as deeper waters along mangrove-lined pools and waterways. Surface-feeding and diving birds would be expected in similar areas as the wading birds. The major difference between mangrove swamps and other coastal ecosystems is the availability of the trunks, limbs, and foliage comprising the tree canopy. This enables a variety of passerine and non-passerine birds, which are not found commonly in other wetland areas, to use mangrove swamps. It also allows extensive breeding activity by a number of tree-nesting birds.

The composition of the avifauna community in mangrove ecosystems is, in fact, highly diverse. Cawkell (1964) recorded 45 species from the mangroves of Gambia (Africa). Haverschmidt (1965) reported 87 species of birds which utilized mangroves in Surinam (S. America). Ffrench (1966) listed 94 species from the Caroni mangrove swamp in Trinidad while Bacon (1970) found 137 in the same swamp. In Malaya, Nisbet (1968) reported 121 species in mangrove swamps and Field (1968) observed 76 from the mangroves of Sierra Leone (Africa).

Use of mangrove ecosystems by birds in Florida has not been recorded in detail. Ninety-two species have been observed in the mangrove habitat of Sanibel Island, Florida (L. Narcisse, J.N. "Ding" Darling Natl. Wildlife Refuge, Sanibel Is., Fla.; personal communication 1981). Robertson (1955) and Robertson and Kushlan (1974) reported on the entire breeding bird fauna of peninsular south Florida, including mangrove regions. Based on limited surveys, these authors reported only 17 species as utilizing mangroves for breeding purposes. Because their studies did not consider migrants or non-breeding residents, a significant fraction of the avifauna community was omitted.

Based on information gleaned from the literature, we have compiled a list of 181 species of birds that use Florida mangrove areas for feeding, nesting, roosting, or other activities (Appendix D). Criteria for listing these species is the same as that used for listing reptiles and amphibians (see Chapter 8 of this volume).

Often references were found stating that a given species in Florida occurred in "wet coastal hammocks", "coastal wet forests" or the like, without a specific reference to mangroves. These species were not included in Appendix D. Thus, this list is a conservative estimate of the avifauna associated with Florida mangrove swamps. Sources for each listing are provided even though many are redundant. Food habit data are based on Howell (1932) and Martin et al. (1951). Estimates of abundance were derived from bird lists published by the U.S. Fish and Wildlife Service for the J.N. "Ding" Darling National Wildlife Refuge at Sanibel Island, Florida, and by the Everglades Natural History Association for Everglades National Park. Frequently, species were recorded from mangrove swamps at one location, but not the other.

We have divided the mangrove avifauna into six groups based on similarities in methods of procuring food. These groups (guilds) are the wading birds, probing shorebirds, floating and diving waterbirds, aerially-searching birds, birds of prey, and arboreal birds. This last group is something of a catch-all group, but is composed mainly of birds that feed and/or nest in the mangrove canopy.

9.2 WADING BIRDS

Herons, egrets, ibises, bitterns, and spoonbills are the most conspicuous group of birds found in mangroves (Figure 14) and are by far the most studied and best understood. Eighteen species (and one important subspecies) are reported from south Florida mangroves.

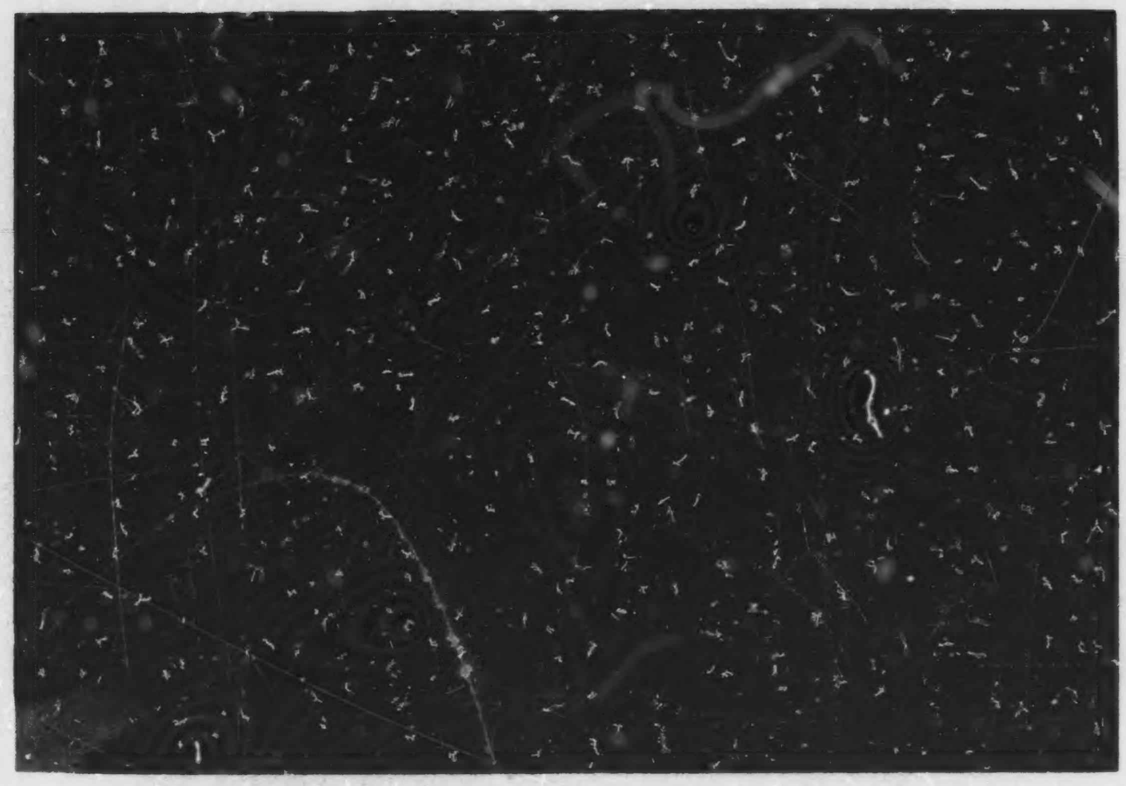


Figure 14. A variety of wading birds feeding in a mangrove-lined pool near Flamingo, Florida. Photograph by David Scott.

Mangrove swamps provide two functions for wading birds. First, they function as feeding grounds. Two-thirds of these species feed almost exclusively on fishes. Although much of their diet is provided by freshwater and non-mangrove marine areas, all of them feed frequently in mangrove swamps. White ibis feed predominantly on crabs of the genus Uca when feeding in mangroves (Kushlan and Kushlan 1975; Kushlan 1979). Mollusks and invertebrates of the sediments are principal foods of the roseate spoonbill although some fish are eaten (Allen 1942). Yellow-crowned night herons and American bitterns eat crabs, crayfish, frogs, and mice in addition to fishes. Snails of the genus Pomacea are fed upon almost exclusively by the limpkin. The sandhill crane is an anomaly in this group since a majority of its food is vegetable matter, especially roots and rhizomes of Cyperus and Sagittaria. Its use of mangroves is probably minimal, occurring where inland coastal marshes adjoin mangroves (Kushlan, unpubl. data). The remaining 12 species are essentially piscivorous although they differ somewhat in the species and sizes of fishes that they consume.

Mangrove swamps also serve as breeding habitat for wading birds. With the exception of the limpkin, sandhill crane, and the two bitterns, all wading bird species in Appendix D build their nests in all three species of mangrove trees (Maxwell and Kale 1977; Girard and Taylor 1979). The species often aggregate in large breeding colonies with several thousand nesting pairs (Kushlan and White 1977a). The Louisiana heron, snowy egret, and cattle egret are the most numerous breeders in south Florida mangroves (based on data in Kushlan and White 1977a).

In wet years over 90% of the south Florida population of white ibis breed in the interior, freshwater wetlands of the Everglades; during these times the mangroves are apparently unimportant, supporting less than 10% of the population (Kushlan 1976, 1977a, b). During drought years, however, production is sustained solely by breeding colonies located in mangroves near the coast (Kushlan 1977a, b). Mangroves are critically important for the survival of the white ibis population even though they appear to be utilized to a lesser extent than freshwater habitats. This pattern of larger but less stable breeding colonies using inland marshes and smaller but more stable colonies using mangroves is also characteristic of heron populations (Kushlan and Frohring, in prep.).

Table 5 gives the number of active nests observed in mangrove regions during the 1974-75 nesting season and the percentage this represents of the entire south Florida breeding population for the nine most abundant species of waders and three associated species. The dependence of roseate spoonbills, great blue herons, Louisiana herons, brown pelicans, and double-crested cormorants on mangrove regions is evident. Nesting by the reddish egret was not quantified during this study although Kushlan and White (1977a) indicated that the only nests of this species which they saw were, in fact, in mangroves. Further observations indicate that this species nests in mangroves exclusively (Kushlan, pers. comm.). Similarly, the great white heron is highly dependent upon mangroves for nesting; they use the tiny mangrove islets which abound along the Florida Keys and in Florida Bay (Howell 1932).

During many years the Everglades population of wood storks is known to nest almost solely in mangroves (Ogden et al. 1976); this population comprises approximately one-third of the total south Florida population. Successful breeding of all these mangrove nesters is undoubtedly correlated with the abundant supply of fishes associated with mangroves. Meeting the energetic demands of growing young is somewhat easier in habitats with abundant prey. This is especially important for the wood stork which requires that its prey be concentrated into small pools by falling water levels during the dry season before it can nest successfully (Kahl 1964; Kushlan et al. 1975; Odgen et al. 1978). Breeding activity by wading birds in mangroves along the southwest and southern Florida

Table 5. Nesting statistics of wading birds and associated species in south Florida, 1974-1975 (based on data in Kushlan and White 1977a).

Species	Active nests in mangroves	% of total active nests in south Florida
White ibis	1914	7
Roseate spoonbill	500	100
Wood stork	1335	31
Great blue heron	458	92
Great egret	1812	39
Snowy egret	2377	46
Little blue heron	71	15
Louisiana heron	3410	70
Cattle egret	2180	13
Brown pelican	741	100
Double-crested cormorant	1744	83

coasts takes place throughout the year (Table 6); at least one species of wader breeds during every month. Colonies on the mangrove islands in Florida Bay were noted to be active nesting sites during all months of the year except September and October (Kushlan and White 1977a).

The seasonal movements of wood storks and white ibises between the various south Florida ecosystems were described by Ogden et al. (1978) and Kushlan (1979). Mangrove ecosystems appear to be most heavily used for feeding in summer (white ibis) and early winter (white ibis and wood stork). The remaining species of wading birds appear to use mangrove areas most heavily in the winter months, reflecting the influx of migrants from farther north.

Wading birds play an important role in nutrient cycling in the coastal mangrove zone. McIvor (pers. observ.) has noted increased turbidity, greater algal biomass, and decreased fish abundance around red mangrove islets with nesting frigate birds and cormorants. Onuf et al. (1977) reported results from a small (100 bird) rookery on a mangrove islet on the east coast of Florida. Additions of ammonium-nitrogen from the bird's droppings exceeded 1 g/m^2/day. Water beneath the mangroves contained five times more ammonium and phosphate than water beneath mangroves without rookeries. Although the wading birds were shown to be a vector for concentrating nutrients, it must be noted that this is a localized phenomenon restricted to the areas around rookeries in the mangrove zone. The effect would be larger around larger rookeries. Onuf et al. (1977) also reported that mangroves in the area of the rookery had increased levels of primary production, higher stem and foliar nitrogen levels, and higher herbivore grazing impact than mangroves without rookeries. Lewis and Lewis (1978) stated that mangroves in large rookeries may eventually be killed due to stripping of leaves and branches for nesting material and by poisoning due to large volumes of urea and ammonia that are deposited in bird guano. This latter effect would be more pronounced in rookeries within mangrove regions subject to infrequent tidal flushing.

9.3 PROBING SHOREBIRDS

Birds in this group are commonly found associated with intertidal and shallow water habitats. Wolff (1969) and Schneider (1978) have shown that plovers and sandpipers are opportunistic feeders, taking the most abundant, proper-sized invertebrates present in whatever habitat the birds happen to occupy.

Of the 25 species included in this guild (Appendix D), two are year-round residents (clapper rail and willet), two breed in mangrove areas (clapper rail and black-necked stilt), and the remainder are transients or winter residents. Baker and Baker (1973) indicated that winter was the most crucial time for shorebirds, in terms of survival. Coincidentally, winter is the time when most shorebirds use mangrove areas. The invertebrate fauna (mollusks, crustaceans, and aquatic insects) which occur on the sediments under intertidal mangroves forms the principal diet of these species. Willets and greater yellowlegs eat a large amount of fishes, especially Fundulus, in addition to invertebrates. Many of the species listed in this guild obtain a significant portion of their energy requirements from other habitats, particularly sandy beaches, marshes, and freshwater prairies. Of the species in this guild, the clapper rail is probably most dependent on mangroves for survival in south Florida (Robertson 1955), although in other geographical locations they frequent salt and brackish marshes.

9.4 FLOATING AND DIVING WATER BIRDS

Twenty-nine species of ducks, grebes, loons, cormorants, and gallinules were identified as populating mangrove areas in south Florida (Appendix D). Eight species are year-round residents while the remainder are present only during migration or as winter visitors.

Table 6. Timing of nesting by wading birds and associated species in south Florida. Adapted from data in Kushlan and White (1977a), Kushlan and McEwan (in press).

Species	Months											
	S	O	N	D	J	F	M	A	M	J	J	A
White ibis	—	—	—	—			—	—	—	—	—	—
Wood stork				—	—	—	—					
Roseate spoonbill			—	—	—	—	—	—				
Great blue/white heron			—	—	—	—	—	—	—	—		
Great egret	—	—	—	—	—	—	—	—	—	—	—	—
Little blue heron							—	—	—	—	—	—
Cattle egret	—	—	—				—	—	—	—	—	—
Double-crested cormorant	—	—	—	—	—	—	—	—	—	—	—	—
Brown pelican				—	—	—	—	—	—	—	—	—

From the standpoint of feeding, members of this guild are highly heterogeneous. Piscivorous species include the cormorant, anhinga, pelicans, and mergansers. Herbivorous species include the pintail, mallard, wigeon, mottled duck, and teals. A third group feeds primarily on benthic mollusks and invertebrates. Scaup, canvasback, redhead, and gallinules belong to this group. The ducks in this last group also consume a significant fraction of plant material.

Species of this guild are permanent residents and usually breed in mangrove swamps. As shown in Table 5, the brown pelican and double-crested cormorant are highly dependent upon mangroves for nesting in south Florida even though both will build nests in any available tree in other geographical regions. It seems that when mangroves are available, they are the preferred nesting site. The anhinga breeds in mangrove regions but is more commonly found inland near freshwater (J. A. Kushlan, So. Fla. Res. Ctr., Everglades Natl. Park, Homestead, Fla.; personal communication 1981). For the other species listed in this guild, mangrove swamps provide a common but not a required habitat; all of these species utilize a variety of aquatic environments.

Kushlan et al. (in prep.) provide recent data on the abundance and distribution of 22 species of waterfowl and the American coot in south Florida estuaries. The American coot is by far the most abundant species, accounting for just over 50% of the total population. Six species of ducks were responsible for more than 99% of the individuals seen: blue-winged teal (41%), lesser scaup (24%), pintail (18%), American wigeon (9%), ring-necked duck (5%), and shoveler (3%). The major habitats included in these authors' surveys were coastal prairie and marshes, mangrove forests, and mangrove-lined bays and waterways of the Everglades National Park.

From these data it appears that waterfowl and coots are most abundant in regions where mangrove, wet coastal prairies, marshes, and open water are interspersed. Overall, the Everglades estuaries support from 5% to 10% of the total wintering waterfowl population in Florida (Goodwin 1979; Kushlan et al. in prep.). As Kushlan et al. point out, however, the Everglades are not managed for single species or groups of species as are areas of Florida supporting larger waterfowl populations. Although the importance of south Florida's mangrove estuaries to continental waterfowl populations may be small, the effect of 70,000 ducks and coots on these estuaries probably is not (Kushlan et al. in prep.).

Kushlan (personal communication) thinks that the estuaries of the Everglades have an important survival value for some segments of the American white pelican population. In winter, approximately 25% of the white pelicans are found in Florida Bay and 75% in the Cape Sable region. They feed primarily in freshwater regions of coastal marshes and prairies and use mangroves where they adjoin this type of habitat.

9.5 AERIALLY-SEARCHING BIRDS

Gulls, terns, the kingfisher, the black skimmer, and the fish crow comprise this guild of omnivorous and piscivorous species (Appendix D). These birds hunt in ponds, creeks, and waterways adjacent to mangrove stands. Many fishes and invertebrates upon which they feed come from mangrove-based food webs. Only six of the 14 species are year-round residents of south Florida. The least tern is an abundant summer resident and the remainder are winter residents or transients.

Only the fish crow actually nests in mangroves. Gulls and terns prefer open sandy areas for nesting (Kushlan and White 1977b) and use mangrove ecosystems only for feeding. All of the species in this guild are recorded from a variety of coastal and inland wetland habitats.

9.6 BIRDS OF PREY

This guild is composed of 20 species of hawks, falcons, vultures, and owls which utilize mangrove swamps in south Florida (Appendix D). The magnificant frigatebird has been included in this group because of its habit of robbing many of these birds of their prey. Prey consumed by this guild includes snakes, lizards, frogs (red-shouldered hawk, swallow-tailed kite), small birds (short-tailed hawk), waterfowl (peregrine falcon, great-horned owl), fishes (osprey, bald eagle), and carrion (black and turkey vultures).

Eleven of these species are permanent residents, one a summer resident, and the remainder are winter residents. Their use of mangrove areas varies greatly. The magnificent frigatebird, which occurs principally in extreme southern Florida and the Florida Keys, utilizes small overwash mangrove islands for both roosts and nesting colonies. Both species of vultures are widely distributed in south Florida mangrove regions; large colonial roosts can be found in mangrove swamps near the coast. Swallow-tailed kites are common over the entire Florida mangrove region (Robertson 1955; Snyder 1974). Snyder (1974) reports extensively on the breeding biology of the swallow-tailed kites in south Florida. The nests he observed were all located in black mangroves although they do nest in other habitats.

The bald eagle, osprey (Figure 15), and peregrine falcon are dependent upon mangrove ecosystems for their continued existence in south Florida. Both the bald eagle and osprey feed extensively on the wealth of fishes found associated with mangrove ecosystems. Additionally, mangroves are used as roosts and support structures for nests. Nisbet (1968) indicated that in Malaysia the most important role of mangroves for birds may be as wintering habitat for palaearctic migrants, of which the peregrine falcon is one. Kushlan (pers. comm.) stated that recent surveys have shown falcons to winter in mangroves, particularly along the shore of Florida Bay where they establish feeding territories. They forage on concentrations of shorebirds and waterfowl. These prey species of the peregrine are common inhabitants of mangrove areas. This could also be true for the merlin, which like the peregrine falcon, feeds on waterfowl and shorebirds. The remaining species in this guild are probably not so dependent on mangroves; although they may be common in mangrove ecosystems, they utilize other habitats as well.

9.7 ARBOREAL BIRDS

This guild is the largest (71 species) and most diverse group inhabiting mangrove forests. Included are pigeons, cuckoos, woodpeckers, flycatchers, thrushes, vireos, warblers, blackbirds, and sparrows. We have lumped this diverse group together because they utilize mangrove ecosystems in remarkably similar ways. Invertebrates, particularly insects, make up a significant portion of most of these birds' diets, although the white-crowned pigeon, mourning dove, and many of the fringilids (cardinal, towhee) eat a variety of seeds, berries, and fruits.

As the name given this guild implies, these birds use the habitat provided by the mangrove canopy. Many birds also use the trunk, branches, and aerial roots for feeding. Several different types of searching patterns are used. Hawking of insects is the primary mode of feeding by the cuckoos, chuck-wills-widows, the kingbirds, and the flycatchers. Gleaning is employed by most of the warblers. Woodpeckers and the prothonotary warbler are classic probers.

Several of the birds in this guild are heavily dependent upon mangrove areas. The prairie warbler and the yellow warbler are subspecies of more widespread North American species (see Appendix D for scientific names). They are found largely within mangrove areas (Robertson and Kushlan 1974). The white-crowned pigeon, mangrove cuckoo, gray kingbird, and black-whiskered vireo are of recent West Indian origin. They first moved into the mangrove-covered regions of south Florida from source areas in the islands of the Caribbean. Confined at first to mangrove

Figure 15. Osprey returning to its nest in a red mangrove tree near Whitewater Bay. Photograph by David Scott.

swamps, all but the mangrove cuckoo have expanded their range in peninsular Florida by using non-mangrove habitat. In this vein it is interesting to note that many species of rare and/or irregular occurrence in south Florida are of West Indian origin and use mangroves to a considerable extent. These include the Bahama pintail, masked duck, Caribbean coot, loggerhead kingbird, thick-billed vireo, and stripe-headed tanager (Robertson and Kushlan 1974).

Twenty-four of the species in this guild are permanent residents, 27 are winter, and 6 are summer residents. Fourteen species are seen only during migrations.

9.8 ASSOCIATIONS BETWEEN MANGROVE COMMUNITY TYPES AND BIRDS

Estimating the degree of use of mangrove swamps by birds as we have done (Appendix D) is open to criticism because of the paucity of information upon which to base judgements. Estimating which mangrove community types (see section 1, Figure 4) are used by which birds is open to even more severe criticism. For this reason the following comments should be regarded as general and preliminary.

In terms of utilization by avifauna, the scrub mangrove swamps are probably the least utilized mangrove community type. Because the canopy is poorly developed, most of the arboreal species are absent, although Emlen (1977) recorded the red-winged blackbird, hairy woodpecker, northern waterthrush, yellow-rumped warbler, common yellowthroat, orange-crowned warbler, palm warbler, yellow warbler, mourning dove, and gray kingbird in scrub mangroves on Grand Bahama Island. Of 25 different habitats surveyed by Emlen (1977), the yellow warbler and gray kingbird were found in the scrub mangroves only. Aerially-searching and wading birds might use scrub mangroves if fishes are present.

Overwash mangrove islands are utilized in a variety of ways by all of the bird guilds. Most of the wading birds plus the magnificent frigatebird, the anhinga, the cormorant, and the brown pelican use overwash islands for nesting (Kushlan and White 1977a). Wading and aerially-searching birds commonly feed in close proximity to overwash islands. A variety of migrating arboreal and probing species use the islands for feeding and roosting. Yellow and palm warblers are common around mangrove islands in Florida Bay as are the black-bellied plover, ruddy turnstone, willet, dunlin, and short-billed dowitcher. Rafts of ducks are common near the inshore islands and birds of prey such as the osprey, the bald eagle, and both vultures use mangrove islands for roosting and nesting.

Fringe and riverine mangrove communities are important feeding areas for wading and probing birds. Floating and diving and aerially-searching birds use the lakes and waterways adjacent to these mangrove communities for feeding. Many of the wading birds nest in fringe and riverine forests. For example, when the wood ibis nests in coastal areas, it uses these mangrove communities almost exclusively (Kushlan, personal communication). Most of the arboreal birds and birds of prey associated with mangroves are found in these two types of communities. This is not surprising since the tree canopy is extremely well-developed and offers roosting, feeding and nesting opportunities.

Hammock and basin mangrove communities are so diverse in size, location, and proximity to other communities that it is difficult to make many general statements about their avifauna. Since there often is little standing water in hammock forests, wading and diving birds probably are not common. Proximity to terrestrial communities in some cases may increase the diversity of arboreal species in both hammock and basin forests; proximity to open areas may increase the likelihood of birds of prey.

It seems safe to conclude that each of the six mangrove community types has some value to the avifauna. This value differs according to community type and kind of bird group under consideration. Certainly, more information is needed, particularly concerning the dependence of rare or endangered species on specific community types.

9.9 MANGROVES AS WINTER HABITAT FOR NORTH AMERICAN MIGRANT LAND BIRDS

An interesting observation based on the data in this chapter is the seemingly important role that mangrove ecosystems play in providing wintering habitat for migrants of North American origin. Lack and Lack (1972) studied the wintering warbler community in Jamaica. In four natural habitats including mangrove forest, lowland dry limestone forest, mid-level wet limestone forest, and montane cloud forest, a total of 174, 131, 61, and 49 warblers (individuals) were seen, respectively. When computed on a per hour of observation basis, the difference is more striking with 22 warblers per hour seen in mangroves and only 1, 2, and 1 seen in the other forest habitats, respectively. For all passerines considered together, 26 passerines/hour were seen in mangroves with 5, 13, and 3 respectively in the other forest habitats. On a species basis only 9 were recorded from mangroves whereas 19, 13, and 16 species, respectively, were seen in the other habitats. This large number of species from the other habitats appears to result from the sighting of rare species after many hours of observation. Only 9 hours were spent by Lack and Lack (1972) in the mangroves whereas between 30 and 86 hours were spent in other habitats. More time in the mangrove zone would have undoubtedly resulted in more species (and individuals) observed (Preston 1979).

Hutto (1980) presented extensive data concerning the composition of migratory land bird communities in Mexico in winter for 13 habitat types. Mangrove areas tended to have more migrant species than most natural habitats (except gallery forests) and also had a greater density of individuals than other habitats (again except for gallery forests). In both Lack and Lack's and Hutto's studies, disturbed and edge habitats had the highest number of species and greatest density of individuals. The percentage of the avifauna community composed of migrants was highest in mangrove habitats, however. From this we can infer the importance of mangroves in the maintenance of North American migrant land birds.

CHAPTER 10. COMMUNITY COMPONENTS - MAMMALS

Thirty-six native and nine introduced species of land mammals occur in the south Florida region (Layne 1974; Hamilton and Whittaker 1979). Of these, almost 50% (18 species) are found in the mangrove zone (Layne 1974). In addition, two species of marine mammals are known from mangrove areas. Data on the abundance and food habits of these 20 species are summarized in Appendix E. All are permanent residents. The criteria for inclusion in this table are similar to those used for the avifauna. Sight records in mangroves or locality data from known mangrove areas were required before a species was included. This has produced a conservative estimate of the mammal species that utilize mangrove areas.

Several mammals do not appear in Appendix E because they have not been recorded from mangrove swamps in south Florida; however, they occur so widely that we suspect they will be found in this habitat in the future. This group includes the cotton mouse, *Peromyscus gossypinus*, the hispid cotton rat, *Sigmodon hispidus*, the round-tailed muskrat, *Neofiber alleni*, the house mouse, *Mus musculus*, the least shrew, *Cryptotis parva*, and the short-tailed shrew, *Blarina brevicauda*.

Few rodents and no bats are included in Appendix E. Compared to the rest of the State, the south Florida region is deficient in these two groups (Layne 1974). Although we have no confirmative field data, we suspect that mangrove swamps along the central and north Florida coasts contain more mammal species, particularly rodents and bats.

A number of medium-sized and large carnivores, including panther, gray fox, bobcat, striped skunk, raccoon, mink, river otter, and black bear, appear to utilize south Florida mangrove areas. Only three of these species (striped skunk, raccoon, and bobcat) are common in mangroves, but several of the rarer species seem to be highly dependent on mangrove swamps. Of 18 recent sightings of the panther in Everglades National Park, 15 were from mangrove ecosystems (Layne 1974). Hamilton and Whittaker (1979) state that it is the coastal hammocks of south Florida, including mangrove areas, which serve to preserve this species in the Eastern United States. Shemnitz (1974) reported that most of the remaining panthers were found in the southwest portion of Florida along the coast and in the interior Everglades regions.

The extent to which other carnivores use mangrove areas varies widely among species. Schwartz (1949) states that mink, although rare, prefer mangroves to other coastal habitats in Florida. Layne (1974, see his figure 1) gives a disjunct distribution for this species in Florida, with the major geographical range being the southwest coast. River otters also utilize mangrove habitat heavily. Otters have been found even far from shore on small mangrove overwash islands in Florida Bay (Layne 1974). Gray fox are not dependent upon mangroves, although they occasionally use this habitat. Less than 20% of all sightings of this species in Everglades National Park were from mangroves (Layne 1974). Bobcat are found in almost all habitats in south Florida from pinelands to dense mangrove forests. The preponderance of recent sightings, however, has been made from the mangrove zone, particularly on offshore mangrove overwash islands (Layne 1974). Black bear are apparently most abundant in the Big Cypress Swamp of Collier County (Shemnitz 1974) and are rare in the remainder of south Florida.

The small mammal fauna of the mangrove zone of south Florida are predominately arboreal and terrestrial species which are adapted to periodic flooding. Opossum, marsh rabbits, cotton rats, and rice rats are commonly found in mangrove swamps. The Cudjoe Key rice rat is a newly described species found only on Cudjoe Key in the Florida Keys. This species appears to be closely associated with stands of white mangroves (Hamilton and Whittaker 1979).

White-tailed deer are common in

Florida mangrove swamps, although they utilize many other habitats. The key deer, a rare and endangered subspecies, is restricted to the Big Pine Key group in the Florida Keys, although it ranged onto the mainland in historical times. Although this little deer makes use of pine uplands and oak hammocks, it extensively exploits mangrove swamps for food and cover.

Two marine mammals, the bottlenose porpoise and the manatee, frequent mangrove-lined waterways. The bottlenose porpoise feeds on mangrove-associated fishes such as the striped mullet, _Mugil cephalus_. Although the manatee feeds primarily upon sea grasses and other submerged aquatic plants, it is commonly found in canals, coastal rivers, and embayments close to mangrove swamps.

Except for the Cudjoe Key rice rat, none of the mammals found in Florida mangroves are solely dependent upon mangrove ecosystems; all of these species can utilize other habitats. The destruction of extensive mangrove swamps would, however, have deleterious effects on almost all of these species. Populations of panther, key deer, and the river otter would probably be the most seriously affected, because they use mangrove habitat extensively.

CHAPTER 11. VALUE OF MANGROVE ECOSYSTEMS TO MAN

Mangrove swamps are often hot, fetid, mosquito-ridden, and almost impenetrable. As a consequence, they are frequently held in low regard. It is possible that more acres of mangrove, worldwide, have been obliterated by man in the name of "reclamation" than any other type of coastal environment. Reclamation, according to Webster's, means "to claim back, as of wasteland". Mangrove swamps are anything but wasteland, however, and it is important to establish this fact before a valuable resource is lost. We can think of six major categories of mangrove values to man; no doubt, there are more.

11.1 SHORELINE STABILIZATION AND STORM PROTECTION

The ability of all three Florida mangroves to trap, hold and, to some extent, stabilize intertidal sediments has been demonstrated repeatedly (reviewed by Scoffin 1970; Carlton 1974). The contemporary view of mangroves is that they function not as "land builders" as hypothesized by Davis (1940) and others, but as "stabilizers" of sediments that have been deposited largely by geomorphological processes (see section 3.2).

Gill (1970), Savage (1972), Teas (1977), and others have emphasized that land stabilization by mangroves is possible only where conditions are relatively quiescent and strong wave action and/or currents do not occur. Unfortunately, no one has devised a method to predict the threshold of physical conditions above which mangroves are unable to survive and stabilize the sediments. Certainly, this depends to some extent on substrate type; mangroves appear to withstand wave energy best on solid rock substrates with many cracks and crevices for root penetration. From our own experience, we suspect that mangroves on sandy and muddy substrates cannot tolerate any but the lowest wave energies, tidal currents much above 25 cm/s, or heavy, regular boat wakes.

The concept that the red mangrove is the best land stabilizer has been questioned by Savage (1972), Carlton (1974), and Teas (1977). These authors argue that the black mangrove (1) is easier to transplant as a seedling, (2) establishes its pneumatophore system more rapidly than the red mangrove develops prop roots, (3) has an underground root system that is better adapted to holding sediments (Teas 1977), (4) is more cold-hardy, and (5) can better tolerate "artificial" substrates such as dredge-spoil, finger fills, and causeways. Generally, the white mangrove is regarded as the poorest land stabilizer of the Florida mangroves (Hanlon et al. 1975).

Although mangroves are susceptible to hurricane damage (see section 12.1), they provide considerable protection to areas on their landward side. They cannot prevent all flooding damage, but they do mitigate the effects of waves and breakers. The degree of this protection is roughly proportional to the width of the mangrove zone. Very narrow fringing forests offer minimal protection while extensive stands of mangroves not only prevent wave damage, but reduce much of the flooding damage by damping and holding flood waters. Fosberg (1971) suggested that the November 1970 typhoon and accompanying storm surge that claimed between 300,000 and 500,000 human lives in Bangladesh might not have been so destructive if thousands of hectares of mangrove swamps had not been replaced with rice paddies.

11.2 HABITAT VALUE TO WILDLIFE

Florida mangrove ecosystems are important habitat for a wide variety of reptiles, amphibians, birds, and mammals (see sections 8, 9, and 10). Some of these animals are of commercial and sport importance (e.g., white-tailed deer, sea turtles, pink shrimp, spiny lobster, snook, grey snapper). Many of these are important to the south Florida tourist industry including the wading birds (e.g., egrets, wood stork, white ibis, herons) which nest in the mangrove zone.

11.3 IMPORTANCE TO THREATENED AND ENDANGERED SPECIES

The mangrove forests of south Florida are important habitat for at least seven endangered species, five endangered subspecies, and three threatened species (Federal Register 1980). The endangered species include the American crocodile, the hawksbill sea turtle, the Atlantic ridley sea turtle, the Florida manatee, the bald eagle, the American peregrine falcon, and the brown pelican. The endangered subspecies are the key deer (*Odocoileus virginianus clavium*), the Florida panther (*Felis concolor coryi*), the Barbados yellow warbler (*Dendroica petechia petechia*), the Atlantic saltmarsh snake (*Nerodia fasciata taeniata*) and the eastern indigo snake (*Drymarchon corais couperi*). Threatened species include the American alligator, the green sea turtle and the loggerhead sea turtle. Although all of these animals utilize mangrove habitat at times in their life histories, species that would be most adversely affected by widespread mangrove destruction are the American crocodile, the Florida panther, the American peregrine falcon, the brown pelican, and the Atlantic ridley sea turtle. The so-called mangrove fox squirrel (*Sciurus niger avicennia*) is widely believed to be a mangrove-dependent endangered species. This is not the case since it is currently regarded as "rare", not endangered, and, further, there is some question whether or not this is a legitimate sub-species (Hall 1981). As a final note, we should point out that the red wolf (*Canis rufus*), which is believed to be extinct in Florida, at one time used mangrove habitat in addition to other areas in south Florida.

11.4 VALUE TO SPORT AND COMMERCIAL FISHERIES

The fish and invertebrate fauna of mangrove waterways are closely linked to mangrove trees through (a) the habitat value of the aerial root structure and (b) the mangrove leaf detritus-based food web (see sections 6 and 7). The implications of these connections were discussed by Heald (1969), Odum (1970), Heald and Odum (1970), and Odum and Heald (1975b) in terms of support for commercial and sport fisheries.

A minimal list of mangrove-associated organisms of commercial or sport value includes oysters, blue crabs, spiny lobsters, pink shrimp, snook, mullet, menhaden, red drum, spotted sea trout, gray and other snapper, tarpon, sheepshead, ladyfish, jacks, gafftopsail catfish, and the jewfish. Heald and Odum (1970) pointed out that the commercial fisheries catch, excluding shrimp, in the area from Naples to Florida Bay was 2.7 million pounds in 1965. Almost all of the fish and shellfish which make up this catch utilize the mangrove habitat at some point during their life cycles. In addition, the Tortugas pink shrimp fishery, which produces in excess of 11 million pounds of shrimp a year (Idyll 1965a), is closely associated with the Everglades estuary and its mangrove-lined bays and rivers.

11.5 AESTHETICS, TOURISM AND THE INTANGIBLES

One value of the mangrove ecosystem, which is difficult to document in dollars or pounds of meat, is the aesthetic value to man. Admittedly, not all individuals find visits to mangrove swamps a pleasant experience. There are many others, however, who place a great deal of value on the extensive vistas of mangrove canopies, waterways, and associated wildlife and fishes of south Florida. In a sense, this mangrove belt along with the remaining sections of the freshwater Everglades and Big Cypress Swamp are the only remaining wilderness areas in this part of the United States.

Hundreds of thousands of visitors each year visit the Everglades National Park; part of the reason for many of these visits includes hopes of catching snook or gray snappers in the mangrove-lined waterways, seeing exotic wading birds, crocodiles, or panthers, or simply discovering what a tropical mangrove forest looks like. The National Park Service, in an attempt to accommodate this last wish, maintains extensive boardwalks and canoe trails through the mangrove forests near Flamingo, Florida. In other, more developed parts of the State, small stands of mangroves or mangrove islands provide a feeling of wilderness in proximity to the rapidly burgeoning urban areas. A variety of tourist attractions including Fairchild Tropical Gardens near Miami and Tiki Gardens near St. Petersburg utilizes the exotic appearance of mangroves as a key ingredient in an attractive landscape. Clearly, mangroves contribute intangibly by diversifying the appearance of south Florida.

11.6 ECONOMIC PRODUCTS

Elsewhere in the world, mangrove forests serve as a renewable resource for many valuable products. For a full discussion of the potential uses of mangrove products, see de la Cruz (in press a), Morton (1965) for red mangrove products, and Moldenke (1967) for black mangrove products.

In many countries the bark of mangroves is used as a source of tannins and dyes. Since the bark is 20% to 30% tannin on a dry weight basis, it is an excellent source (Hanlon et al. 1975). Silviculture (forestry) of mangrove forests has been practiced extensively in Africa, Puerto Rico, and many parts of Southeast Asia (Holdridge 1940; Noakes 1955; Macnae 1968; Walsh 1974; Teas 1977). Mangrove wood makes a durable and water resistant timber which has been used successfully for residential buildings, boats, pilings, hogsheads, fence posts, and furniture (Kuenzler 1974; Hanlon et al. 1975). In Southeast Asia mangrove wood is widely used for high quality charcoal.

Morton (1965) mentions that red mangrove fruits are somtimes eaten by humans in Central America, but only by populations under duress and subject to starvation. Mangrove leaves have variously been used for teas, medicinal purposes, and livestock feeds. Mangrove teas must be drunk in small quantities and mixed with milk because of the high tannin content (Morton 1962); the milk binds the tannins and makes the beverage more palatable.

As a final note, we should point out that mangrove trees are responsible for contributing directly to one commercial product in Florida. The flowers of black mangroves are of considerable importance to the three million dollar (1965 figures) Florida honey industry (Morton 1964).

Other than the honey industry, most of these economic uses are somewhat destructive. There are many cases in which clear-cut mangrove forests have failed to regenerate successfully for many years because of lack of propagule dispersal or increased soil salinities (Teas 1979). We believe that the best use of Florida mangrove swamps will continue to be as preserved areas to support wildlife, fishing, shoreline stabilization, endangered species, and aesthetic values.

CHAPTER 12. MANAGEMENT IMPLICATIONS

12.1 INHERENT VULNERABILITY

Mangroves have evolved remarkable physiological and anatomical adaptations enabling them to flourish under conditions of high temperatures, widely fluctuating salinities, high concentrations of heavy metals (Walsh et al. 1979), and anaerobic soils. Unfortunately, one of these adaptations, the aerial root system, is also one of the plant's most vulnerable components. Odum and Johannes (1975) have referred to the aerial roots as the mangrove's Achilles' heel because of their susceptibility to clogging, prolonged flooding, and boring damage from isopods and other invertebrates (see section 6 for a discussion of the latter). This means that any process, natural or man-induced, which coats the aerial roots with fine sediments or covers them with water for extended periods has the potential for mangrove destruction. Bacon (1970) mentions a case in Trinidad where the Caroni River inundated the adjacent Caroni Mangrove Swamp during a flood and deposited a layer of fine red marl in a large stand of black mangroves which subsequently died. Many examples of damage to mangrove swamps from human activities have been documented (see section 12.2).

One of the few natural processes that causes periodic and extensive damage to mangrove ecosystems is large hurricanes (Figure 16). Craighead and Gilbert (1962) and Tabb and Jones (1962) have documented the impact of Hurricane Donna in 1960 on parts of the mangrove zone of south Florida. Craighead and Gilbert (1962) found extensive damage over an area of 100,000 acres (40,000 ha). Loss of trees ranged from 25% to 100%. Damage occurred in three ways: (1) wind shearing of the trunk 6 to 10 ft (2 to 3 m) above ground, (2) overwash mangrove islands being swept clean, and (3) trees dying months after the storm, apparently in response to damage to the prop roots from coatings by marl and fine organic matter. The latter type of damage was most widespread, but rarely occurred in intertidal forests, presumably because the aerial roots were flushed and cleaned by tidal action. Fish and invertebrates were adversely affected by oxygen depletion due to accumulations of decomposing organic matter (Tabb and Jones 1962).

Hurricane Betsy in 1965 did little damage to mangroves in south Florida; there was also little deposition of silt and marl within mangrove stands from this minimal storm (Alexander 1967). Lugo et al. (1976) have hypothesized that severe hurricanes occur in south Florida and Puerto Rico on a time interval of 25 to 30 years and that mangrove ecosystems are adapted to reach maximum biomass and productivity on the same time cycle.

12.2 MAN-INDUCED DESTRUCTION

Destruction of mangrove forests in Florida has occurred in various ways including outright destruction and land filling, diking and flooding (Figure 17), through introduction of fine particulate material, and pollution damage, particularly oil spills. To our knowledge there are no complete, published documented estimates of the amount of mangrove forests in Florida which have been destroyed by man in this century. Our conclusion is that total loss statewide is not too great, probably in the range of 3 to 5% of the original area covered by mangroves in the 19th century, but that losses in specific areas, particularly urban areas, are appreciable. This conclusion is based on four pieces of information. (1) Lindall and Saloman (1977) have estimated that the total loss of vegetated intertidal marshes and mangrove swamps in Florida due to dredge and fill is 23,521 acres (9,522 ha); remember that there are between 430,000 and 500,000 acres (174,000 to 202,000 ha) of mangroves in Florida (see section 1.3). (2) Birnhak and Crowder (1974) estimate a loss of approximately 11,000 acres (4,453 ha) of mangroves between 1943 and 1970 in three counties (Collier, Monroe, and Dade). (3) An obvious loss of mangrove forests has occurred in Tampa Bay, around Marco Island, in the Florida Keys, and along the lower east coast of Florida. For example, Lewis et al. (1979) estimated that 44% of the intertidal vegetation

Figure 16. Damaged stand of red and black mangroves near Flamingo, Florida, as it appeared 7 years after Hurricane Donna.

Figure 17. Mangrove forest near Key West as it appeared in 1981 after being destroyed by diking and impounding.

including mangroves in the Tampa Bay estuary has been destroyed during the past 100 years. (4) Heald (unpublished MS.) has estimated a loss of 2,000 acres (810 ha) of mangroves within the Florida Keys (not considered by Birnhak and Crowder 1974). So while loss of mangrove ecosystems throughout Florida is not overwhelming, losses at specific locations have been substantial.

Diking, impounding, and long-term flooding of mangroves with standing water can cause mass mortality, especially when prop roots and pneumatophores are covered (Breen and Hill 1969; Odum and Johannes 1975; Patterson-Zucca 1978; Lugo 1981). In south Florida, E. Heald (pers. comm.) has observed that permanent impoundment by diking which prevents any tidal exchange and raises water levels significantly during the wet season will kill all adult red and black mangrove trees. If conditions behind the dike remain relatively dry, the mangroves may survive for many years until replaced by terrestrial vegetation.

Mangroves are unusually susceptible to herbicides (Walsh et al. 1973). At least 250,000 acres (100,000 ha) of mangrove forests were defoliated and killed in South Viet Nam by the U.S. military. This widespread destruction has been documented by Tschirley (1969), Orians and Pfeiffer (1970), Westing (1971), and a committee of the U.S. Academy of Sciences (Odum et al. 1974). In many cases these forests were slow to regenerate; observations by de Sylva and Michel (1974) indicated higher rates of siltation, greater water turbidity, and possibly lower dissolved oxygen concentrations in swamps which sustained the most damage. Teas and Kelly (1975) reported that in Florida the black mangrove is somewhat resistant to most herbicides but the red mangrove is extremely sensitive to herbicide damage. He hypothesized that the vulnerability of the red mangrove is related to the small reserves of viable leaf buds in this tree. Following his reasoning, the stress of a single defoliation is sufficient to kill the entire tree.

Although mangroves commonly occur in areas of rapid sedimentation, they cannot survive heavy loads of fine, floculent materials which coat the prop roots. The instances of mangrove death from these substances have been briefly reviewed by Odum and Johannes (1975). Mangrove deaths from fine muds and marl, ground bauxite and other ore wastes, sugar cane wastes, pulp mill effluent, sodium hydroxide wastes from bauxite processing, and from intrusion of large quantities of beach sand have been documented from various areas of the world.

12.3 EFFECTS OF OIL SPILLS ON MANGROVES

There is little doubt that petroleum and petroleum byproducts can be extremely harmful to mangroves. Damage from oil spills has been reviewed by Odum and Johannes (1975), Carlberg (1980), Ray (in press), and de la Cruz (in press, b). Over 100 references detailing the effects of oil spills on mangroves and mangrove-associated biota are included in these reviews.

Petroleum and its byproducts injure and kill mangroves in a variety of ways. Crude oil coats roots, rhizomes, and pneumatophores and disrupts oxygen transport to underground roots (Baker 1971). Various reports suggest that the critical concentration for crude oil spills which may cause extensive damage is between 100 and 200 ml/m^2 of swamp surface (Odum and Johannes 1975). Petroleum is readily absorbed by lipophylic substances on surfaces of mangroves. This leads to severe metabolic alterations such as displacement of fatty molecules by oil hydrocarbons leading to destruction of cellular permeability and/or dissolution of hydrocarbons in lipid components of chloroplasts (Baker 1971).

As with other intertidal communities, many of the invertebrates, fishes, and plants associated with the mangrove community are highly susceptible to petroleum products. Widespread destruction of organisms such as attached algae, oysters, tunicates, crabs, and gobies have been reported in the literature (reviewed by de

la Cruz in press, b; Ray in press).

Damage from oil spills follows a predictable pattern (Table 7) which may require years to complete. It is important to recognize that many of the most severe responses, including tree death, may not appear for months or even years after the spill.

In Florida, Chan (1977) reported that red mangrove seedlings and black mangrove pneumatophores were particularly sensitive to an oil spill which occurred in the Florida Keys. Lewis (1979a, 1980b) has followed the long-term effects of a spill of 150,000 liters (39,000 gal) of bunker C and diesel oil in Tampa Bay. He observed short-term (72-hour) mortality of invertebrates such as the gastropod Melongena corona and the polychaete Laeonereis culveri. Mortality of all three species of mangroves began after three weeks and continued for more than a year. Sublethal damage included partial defoliation of all species and necrosis of black mangrove pneumatophores; death depended upon the percentage of pneumatophores affected.

In addition to the damage from oil spills, there are many adverse impacts on mangrove forests from the process of oil exploration and drilling (Table 8). This type of damage can often be reduced through careful management and monitoring of drilling sites.

Although little is known concerning ways to prevent damage to mangroves once a spill has occurred, protection of aerial roots seems essential. Prop roots and pneumatophores must be cleaned with compounds which will not damage the plant tissues. Dispersants commonly used to combat oil spills are, in general, toxic to vascular plants (Baker 1971). If possible, oil laden spray should not be allowed to reach leaf surfaces. Damage during clean-up (e.g., trampling, compaction, bulldozing) may be more destructive than the untreated effects of the oil spill (de la Cruz in press, b).

12.4 MAN-INDUCED MODIFICATIONS

In south Florida, man has been responsible for modifications which, while not killing mangroves outright, have altered components of the mangrove ecosystem. One of the most widespread changes involves the alteration of freshwater runoff. Much of the freshwater runoff of the Florida Everglades has been diverted elsewhere with the result that salinities in the Everglades estuary are generally higher than at the turn of the century. Teas (1977) points out that drainage in the Miami area has lowered the water table as much as 2 m (6 ft).

Interference with freshwater inflow has extensive effects on estuaries (Odum 1970). Florida estuaries are no exception; the effects on fish and invertebrate species along the edge of Biscayne and Florida Bays have been striking. The mismanagement of freshwater and its effects on aquatic organisms have been discussed by Tabb (1963); Idyll (1965a,b); Tabb and Yokel (1968) and Idyll et al. (1968). In addition, Estevez and Simon (1975) have hypothesized that the impact of the boring isopod, Sphaeroma terebrans, may be more severe when freshwater flows from the Everglades are altered.

One generally unrecognized side effect of lowered freshwater flow and salt water intrusion has been the inland expansion of mangrove forests in many areas of south Florida. There is documented evidence that the mangrove borders of Biscayne Bay and much of the Everglades estuary have expanded inland during the past 30 to 40 years (Reark 1975; Teas 1979; Ball 1980).

Sections of many mangrove forests in south Florida have been replaced by filled residential lots and navigation canals. Although these canal systems have not been studied extensively, there is some evidence, mostly unpublished, that canals are not as productive in terms of fishes and invertebrates as the natural mangrove-lined waterways which they replaced.

Table 7. General response of mangrove ecosystems to severe oil spills (from Lewis 1980b)

Stage	Observed impact
Acute	
0 to 15 days	Deaths of birds, turtles, fishes, and invertebrates
15 to 30 days	Defoliation and death of small mangroves, loss of aerial root community
Chronic	
30 days to 1 year	Defoliation and death of medium-sized mangroves (1 - 3 m), tissue damage to aerial roots
1 year to 5 years	Death of large mangroves (greater than 3 m), loss of oiled aerial roots, and regrowth of new roots (often deformed)
	Recolonization of oil-damaged areas by new seedlings
1 year to 10 years (?)	Reduction in litter fall, reduced reproduction, and reduced survival of seedlings
	Death or reduced growth of young trees colonizing spill site (?)
	Increased insect damage (?)
10 to 50 years (?)	Complete recovery

Table 8. Estimated impact of various stages of oil mining on mangrove ecosystems (modified from Longley et al. 1978 and de la Cruz in press,b).

Stage	Activity	Impacts
Pre-exploration	Seismic surveys Clearing of survey lines Drilling "shot lines"	Crushing and clearing vegetation Vehicle track compaction Damage to natural levees
Site preparation	Canal excavation Dredge spoil deposition Road construction	Loss of habitat in disturbed areas Alteration of water flow pathways Increased turbidity, higher rates of sedimentation, and lowered dissolved oxygen in nearby waters
Drilling	Increased activity at site related to drilling	Continued high turbidity Release of toxic substances Displacement of wildlife
Production	Construction of platforms Construction of pipelines Maintenance dredging Placement of tanks and other equipment	Continued high turbidity Loss of additional habitat Further changes in wetland drainage patterns from pipeline construction Release of toxic substances Oil spills
Oil spills	Oil leaks and spills due to well blow-out, pipeline breakage, carelessness, and barge rupture Clean-up activities	Destruction of plant and animal populations Alteration of ecosystem processes such as primary production and decomposition Introduction of persistent toxic substances into soils

Weinstein et al. (1977) found that artificial canals had lower species diversity of benthic infauna and trawl-captured fishes and generally finer sediments than the natural communities. Courtney (1975) reported a number of mangrove-associated invertebrates which did not occur in the artificial channels.

Mosquito production is a serious problem in black mangrove-dominated swamps in Florida (Provost 1969). The salt marsh mosquitos, *Aedes taeniorhynchus* and *A. sollicitans*, do not reproduce below the mean high tide mark and for this reason are not a serious problem in the intertidal red mangrove swamps. Mosquitos lay their eggs on the damp soil of the irregularly flooded black mangrove zone; these eggs hatch and develop when flooded by spring tides, storm tides or heavy rains. As with the "high marsh" of temperate latitudes, there have been some attempts to ditch the black mangrove zone so that it drains rapidly after flooding. Although properly designed ditching does not appear to be particularly harmful to mangrove swamps (other than the area destroyed to dig the ditch and receive the spoil), it is an expensive practice and for this reason is not widely practiced. Properly managed diking can be an effective mosquito control approach with minimal side effects to black mangroves (Provost 1969). Generally, ditching or diking of the intertidal red mangrove zone is a waste of money.

Mangrove swamps have been proposed as possible tertiary treatment areas for sewage (see discussion by Odum and Johannes 1975). To our knowledge, this alternate use is not currently practiced in south Florida. Until more experimental results are available on the assimilative capacities and long-term changes to be expected in mangrove forests receiving heavy loads of secondary treated sewage, it would be an environmental risk to use mangrove forests for this purpose.

In many areas of the world mangrove swamps have been converted to other uses such as aquaculture and agriculture (see de la Cruz, in press, a). Although some of the most productive aquaculture ponds in Indonesia and the Philippines are located in former mangrove swamps, there is some question whether the original natural system was not equally productive in terms of fisheries products at no cost to man (Odum 1974). Conversion to aquaculture and agriculture is cursed with a variety of problems including subsequent land subsidence and the "cat clay" problem. The latter refers to the drastically lowered soil pH which often occurs after drainage and has been traced to oxidation of reduced sulfur compounds (Dent 1947; Tomlinson 1957; Hesse 1961; Hart 1962, 1963; Moorman and Pons 1975). Experience in Africa, Puerto Rico, and Southeast Asia confirms that mangrove forests in their natural state are more valuable than the "reclaimed" land.

12.5 PROTECTIVE MEASURES INCLUDING TRANSPLANTING

Protection of mangroves includes (1) prevention of outright destruction from dredging and filling; (2) prevention of drainage, diking and flooding (except for carefully managed mosquito control); (3) prevention of any alteration of hydrological circulation patterns, particularly involving tidal exchange; (4) prevention of introduction of fine-grained materials which might clog the aerial roots, such as clay, and sugar cane wastes; (5) prevention of oil spills and herbicide spray driftage; and (6) prevention of increased wave action or current velocities from boat wakes, and sea walls.

Where mangroves have been destroyed, they can be replanted or suitable alternate areas can be planted, acre for acre, through mitigation procedures (see Lewis et al. 1979). An extensive body of literature exists concerning mangrove planting techniques in Florida (Savage 1972; Carlton 1974; Pulver 1976; Teas 1977; Goforth and Thomas 1979; Lewis 1979b). Mangroves were initially planted in Florida at least as early as 1917 to protect the overseas railway in the Florida Keys (Teas 1977).

Both red and black mangroves have

been used in transplanting. As we mentioned in section 11, black mangroves seem to have certain advantages over red mangroves. Properly designed plantings are usually 75% to 90% successful, although the larger the transplanted tree, the lower its survival rate (Teas 1977). Pruning probably enhances survival of trees other than seedlings (Carlton 1974). Important considerations (Lewis 1979b; Teas 1977) in transplanting mangroves are: (1) to plant in the intertidal zone and avoid planting at too high or too low an elevation, (2) to avoid planting where the shoreline energy is too great, (3) to avoid human vandalism, and (4) to avoid accumulations of dead sea grass and other wrack.

Costs of transplanting have been variously estimated. Teas (1977) suggests $462 an acre ($1,140/ha) for unrooted propagules planted 3 ft (0.9 m) apart, $1,017 an acre ($2,500/ha) for established seedlings planted 3 ft (0.9 m) apart and $87,500 ($216,130/ha) for 3 year-old nursery trees planted 4 ft (1.2 m) apart. Lewis (1979b) criticized Teas' costs as unrealistically low and reported a project in Puerto Rico which used established seedlings at a cost of $5,060 an acre ($12,500/ha); he did suggest that this cost could be cut in half for larger projects.

12.6 ECOLOGICAL VALUE OF BLACK VS. RED MANGROVES

One unanswered question of current interest in Florida concerns the ecological value of black mangrove forests compared to intertidal red mangrove forests. In many respects, this is identical to the "high marsh" versus "low marsh" debate in temperate wetlands. One hypothetical argument which has been presented frequently in court cases during the past decade suggests that black mangrove forests have less ecological value than red mangrove forests to both man and coastal ecosystems. This argument is based on an apparent lack of substantial particulate detritus export from black mangrove forests above mean high tide and the generally perceived lack of organisms, particularly gamefishes, which use black mangrove forests as habitat.

The counter argument states that black mangrove forests are important for the support of wildlife and the export of substantial quantities of dissolved organic matter (DOM). Lugo et al. (1980) provide evidence that black mangrove forests do, in fact, export large quantities of DOM. They point out that (1) black mangrove leaves decompose more rapidly than red mangrove leaves and thus produce relatively more DOM and (2) absolute export of carbon from these forests, on a statewide scale, is equal or greater than from red mangrove forests.

12.7 THE IMPORTANCE OF INTER-COMMUNITY EXCHANGE

From previous discussions (sections 6 and 7.5 and Appendices B, C, D and E) it is clear that many species of fishes, invertebrates, birds, and mammals move between mangrove forest communities and other habitats including sea grass beds, coral reefs, terrestrial forests, and the freshwater Everglades. For example, the gray snapper, *Lutjanus griseus*, spends part of its juvenile life in sea grass beds, moves to mangrove-lined bays and rivers, and then migrates to deeper water and coral reefs as an adult (Croaker 1962; Starck and Schroeder 1971). The pink shrimp, *Penaeus duorarum*, spends its juvenile life in mangrove-lined bays and rivers before moving offshore to the Tortugas grounds as an adult. During its juvenile period it appears to move back and forth from mangrove-dominated areas to sea grass beds. The spiny lobster, *Panulirus argus*, as a juvenile frequently uses mangrove prop root communities as a refuge; when nearing maturity this species moves to deeper water in sea grass and coral reef communities (see discussion section 6.1). Many of the mammals (section 10) and birds (section 9) move back and forth between mangrove communities and a variety of other environments.

These are only a few of many

examples. Clearly, mangrove ecosystems are linked functionally to other south Florida ecosystems through physical processes such as water flow and organic carbon flux. As a result, the successful management and/or preservation of many fishes, mammals, birds, reptiles, and amphibians depends on proper understanding and management of a variety of ecosystems and the processes that link them. Saving mangrove stands may do the gray snapper little good if sea grass beds are destroyed. Pink shrimp populations will be enhanced by the preservation of sea grass beds and mangrove-lined waters, but shrimp catches on the Tortugas grounds will decline if freshwater flow from the Everglades is not managed carefully (Idyll et al. 1968). Successful management of south Florida mangrove ecosystems, including their valuable resources, will depend on knowledgeable management of a number of other ecosystems and the processes which link them.

12.8 MANAGEMENT PRACTICES: PRESERVATION

Based on years of research in south Florida and based on the information reviewed for this publication, we have concluded that the best management practice for all types of Florida mangrove ecosystems is preservation. Central to this concept is the preservation of adjacent ecosystems that are linked significantly by functional processes. The continued successful functioning of the mangrove belt of southwest Florida is highly dependent on the continual existence of the Everglades and Big Cypress Swamp in an ecologically healthy condition.

At no cost to man, mangrove forests provide habitat for valuable birds, mammals, amphibians, reptiles, fishes, and invertebrates and protect endangered species, at least partially support extensive coastal food webs, provide shoreline stability and storm protection, and generate aesthetically pleasing experiences (Figure 18). In situations where overwhelming economic pressures dictate mangrove destruction, every effort should be made to ameliorate any losses either through mitigation or through modified development as described by Voss (1969) and Tabb and Heald (1973) in which canals and seawalls are placed as far to the rear of the swamp as possible.

Figure 18. Mangrove islands in Florida Bay near Upper Matecumbe Key. Note the extensive stands of seedling red mangroves which have become established (1981) after a long period without major hurricanes. Mangrove islands in the Florida Keys tend to expand during storm-free intervals.

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APPENDIX A. Summary of the site characteristics and sampling methodology for fishes in: A-1 - mangrove-fringed tidal streams and rivers, A-2 - mangrove-lined estuarine bays and lagoons, and A-3 - mangrove-lined oceanic bays and lagoons.

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Table A-1. Site characteristics and sampling methodology for fishes in mangrove-fringed tidal streams and rivers.

Location	Salinity range	Temperature range	Mean depth; tidal range	Substrate	Benthic vegetation	Sampling methods	Frequency	Number species recorded
North River; Tabb 1966, Odum 1970	0-27 o/oo	15.4°-33.2°C	1 m; 0.5 m	Largely exposed limestone, and sand banks; undercut mangrove peat	Scattered *Ruppia maritima* near mouth	Bag seine, throw nets, dip nets, traps, pound net, fish poison, rod & reel, trammel net, set lines	Monthly, Sept. 1965 through Sept. 1966 (Tabb)	55
Cross Bayou Canal (Boca Ciega Bay to Old Tampa Bay); Springer & Woodburn 1960	3.2-29.8 o/oo	13.0°-31.5°C	Max. depth 1.5 m; 0.9 m	Hard muddy sand	Sparse *Enteromorpha*	Bag seine; minnow seine	Monthly, Sept. 1957 through Dec. 1958	60
Fahkahatchee stream, stream entering Fahka Union Canal; Carter et al. 1973	2-36 o/oo	22°-29°C	Less than 1 m; range not given	Not given	Not given	Seines routinely; black net & rotenone for single standing crop estimate	Monthly, Jan. 1972 through Dec. 1972	47
Unnamed streams near Turkey Point, Biscayne Bay; Nugent 1970	16-32 o/oo	13.2°-37.1°C	1.1 m; 0.5 m	Thick organic mud-gill net & trap sites; culvert at hoop net sites	Dense *Thalassia testudinum* at mouth	Gill nets; hoop nets; traps	Weekly, gill nets; bimonthly, others; August 1968 through Dec. 1969	52
							Total	111
							Only taken in SE Fla.	-23
								88

Table A-2. Site characteristics and sampling methodology for fishes in mangrove-lined estuarine bays and lagoons.

Location	Salinity range	Temperature range	Mean depth; tidal range	Substrate	Benthic vegetation	Sampling methods	Frequency	Number species recorded
Fahkahatchee Bay, 740 ha; Yokel 1975b, Carter et al. 1973	Average - 15-37 o/oo, low of 1 o/ooo recorded by Yokel, Sept. 1971	21°-31°C (Yokel); 23.5°-32°C (Carter et al.)	1.2 m; ---.	Generally muddy, some sand & shell	Extensive areas of *Halodule wrightii*, *Thalassia testudinum* in northern portion	Vegetated, mud, sand/shell bottoms sampled by otter trawl (Yokel); 2 bag seines, otter trawl, surface trawl (Carter et al.)	Monthly, July 1971 through July 1972 (Yokel); Monthly, Jan. 1972 through Dec. 1972 (Carter et al.)	47 (Yokel) 89[a]
Fahka Union Bay, 186 ha; Carter et al. 1973	5-35 o/oo subject to sporadic massive freshwater inputs from GAC[b] drainage canals	24°-32.5°C	1.0 m; ---	Muddy, occasional sandy area or oyster bar	Little seagrass, high standing crop of green algae	2 bag seines, otter trawl, surface trawl	Monthly, Jan. 1972 through Dec. 1972	89[a]
Rookery Bay, 419 ha; Yokel 1975a	8.9-38.5 o/oo	14.3°-31.8°C	0.9 m; .55 m	Mud, sand, shell	*Halodule wrightii*, *Thalassia testudinum*, *Halophila engelmannii*	Vegetated, mud, sand/shell bottoms sampled by other trawl	Monthly, June 1970 through July 1972	64
Marco Island Estuary; Yokel 1975b; Weinstein et al. 1977	19 o/oo Sept. 1971; otherwise over a 4-yr period 29-39 o/oo	13°-32°C	Not given	Mud, muddy sand, shelly sand	*Halodule wrightii* beds in shallow back-bays of mangrove complex; *Thalassia* not well developed	Vegetated, mud, sand/shell bottoms sampled by otter trawl (Yokel); otter trawl (Weinstein et al.)	Monthly, July 1971 through July, 1972 (Yokel); Monthly, July 1971 through Jan. 1975 (Weinstein et al.)	59 (Yokel) 82; (Weinstein)
Whitewater Bay, Clark 1970	2.9-29.3 o/oo	15.9°-32.1°C	Shallow stations-1 m, deep stations-0.8-1.0 m; 0.6 m	Peat, silt, marl & shell, sand & shell	*Halodule wrightii*, *Udotea conglutinata*, *Chara hornemanni*, *Dasya pedicellata*, *Gracilaria* sp., *Halophila baillonis*	Roller frame trawl	Monthly - 8 stations Sept. 1968 through Nov. 1969	67
							Total	117

[a] 89 species in Fahkahatchee and Fahka Union Bays combined.
[b] Gulf American Corporation.

Table A-3. Site characteristics and sampling methodology for fishes in mangrove-lined oceanic bays and lagoons.

Location	Salinity range	Temperature range	Mean depth; tidal range	Substrate	Benthic vegetation	Sampling methods	Frequency	Number species recorded
Old Rhodes Key Lagoon, Holm 1977	Average April-June 1973 - 37 o/oo	Average for Apr.-June, 1973 - 28°C	0.61 m; 0.5 m range		Seagrasses: *Thalassia testudinum*	Visual counts, traps, hook and line	Monthly, 1973	31
Porpoise Lake, Florida Bay, Hudson et al. 1970	27.8-49.6 o/oo	16.6°-32.2°C	Max. depth - 2.1 m; ---	Carbonate mud & shell fragments	Seagrasses: extensive *Thalassia testudinum*, sparse *Halodule wrightii*	Suction sampler, slednet, pushnet, beach seine, cast net, roller-frame trawls, hook & line	Monthly, April 1965 through Jan. 1968	64
Southern Biscayne Bay, Bader and Roessler 1971	5.0-43.8 o/oo	13.5°-38.7°C[a]	Range 1.0-2.5 m	Mud, sand, coarse sand & shell fragments	Seagrasses: *Thalassia testudinum*, *Halodule wrightii*, red algae-*Laurencia*, *Digenia*	Otter trawl	Monthly, July 1968 through June 1970	75
Western Florida Bay 316 km^2, Schmidt 1979	Not given	Not given	Not given	Not given	Not given though author states each representative benthic habitat was sampled	Bag seine, semi-balloon otter trawl	Monthly, May 1973 through June 1974 at 12 stations	109
							Total	156

[a] Some sampling stations were within the area of the thermal plume from the Turkey Point power plant, temperature elevation up to 5.2°C above ambient.

APPENDIX B. Fishes of mangrove areas of Florida tabulated by habitat type. Key to numbered references appears at the end of the table. Diet items listed in order of decreasing importance.

Family and Species	Habitat Type Tidal Stream	 Estuarine Bay	 Oceanic Bay	Reference	Diet	Diet Reference	Comments
Orectolobidae - carpet sharks							
Ginglymostoma cirratum nurse shark	+		+	1, 5, 7	Fish, cephalopods, molluscs, shrimp, sea urchins	Randall 1967 Clark & von Schmidt 1965 Bohlke & Chaplin 1968	
Carcharhinidae - requiem sharks							
Carcharhinus leucas bull shark	+			8	Juveniles: fish (*Arius felis*, *Lophogobius*, *Mugil cephalus*, *Brevoortia patronus*, *Micropogon undulatus*), crustaceans including penaeid shrimp, blue crabs	Odum 1971[a]	
Carcharhinus limbatus blacktip shark			+	11	Fish (*Caranx* sp., *Centropomus undecimalis*, *Chilomycterus schoepfi*, *Arius felis*, *Lactophrys trigonus* *Lagodon rhomboides*), crabs	Clark & von Schmidt 1965	
Negaprion brevirostris lemon shark	+		+	4, 5, 7	Young: crustaceans, fish Adults: fish, crustaceans	Randall 1967 Clark & Von Schmidt 1965	
Sphyrnidae - hammerhead sharks							
Sphyrna tiburo - bonnethead		+	+	2, 5	Mantis shrimp, shrimp, isopods, barnacles, bivalve molluscs, cephalopods, fish	Bohlke & Chaplin 1968	
Pristidae - sawfishes							
Pristis pectinata smalltooth sawfish	+		+	5, 15	Fish, benthic crustaceans	Bohlke & Chaplin 1968	
Rhinobatidae - guitarfishes							
Rhinobatos lentiginosus - Atlantic guitarfish			+	1			
Torpedinidae - electric rays							
Narcine brasiliensis - lesser electric ray		+	+	1, 17, 18			
Rajidae - skates					Crustacea, fish, annelids	Reid 1954	
Raja texana roundel skate			+	1			
Dasyatidae - stingrays							
Dasyatis americana - southern stingray	+	+	+	2, 4, 5, 7	Fishes, sipunculid and polychaete worms, crabs, bivalves, shrimp, mantis shrimp	Randall 1967	
Dasyatis sabina Atlantic stingray	+	+		2, 8, 13, 17	Benthic invertebrates including bivalves, xanthid and portunid crabs, shrimps, amphipods, annelids, chironomid larvae	Darnell 1958	
Gymnura micrura - smooth butterfly ray		+		17	Fish, molluscs, annelids, shrimp, other small crustaceans	Peterson & Peterson 1979	
Urolophus jamaicensis - yellow stingray			+	1	Probably small burrowing invertebrates	Bohlke & Chaplin 1968	

[a] This and all subsequent Odum 1971 citations refer to W.E. Odum 1971.

Family and Species	Habitat Type Tidal Stream	 Estuarine Bay	 Oceanic Bay	Reference	Diet	Diet Reference	Comments
Myliobatidae - eagle rays							
Aetobatus narinari - spotted eagle ray		+		2	Clams, oysters	Bohlke & Chaplin 1968	
Lepisosteidae - gars							
Lepisosteus platyrhincus - Florida gar	+			2, 7, 13, 15	Fish (poeciliids, cyprinodonts, small centrarchids), crustaceans (caridean shrimp), insect larvae	Odum 1971	
Elopidae - tarpons							
Elops saurus - ladyfish	+	+	+	2, 3, 7, 8, 13, 15	< 45 mm: zooplankton, chaetognaths, polychaete worms > 45 mm: caridean & penaeid shrimp, various small fish	Odum 1971 Austin & Austin 1971	
Megalops atlantica - tarpon	+	+	+	7, 8, 13, 15	< 45 mm: plankton (cyclopoid copepods) juveniles: fish (*Gambusia*, *Fundulus heteroclitus*, *Mugil cephalus*), crustaceans (ostracods, caridean shrimp) adults: wide variety of fish, crabs, shrimp, ctenophores, insects	Odum 1971 Austin & Austin 1971	Obligate air breathers. Juveniles inhabit shallow brackish pools low in oxygen, often containing H_2S (Wade 1962)
Albulidae - bone fishes							
Albula vulpes - bonefish			+	4, 5	Clams, snails, shrimp, small fish	Bohlke & Chaplin 1968	
Anguillidae - eels							
Anguilla rostrata - American eel	+			8, 13	50-200 mm: amphipods, isopods 180-472 mm: xanthid crabs, caridean shrimp, fish (*Lophogobius cyprinoides*)	Odum 1971	
Ophichthidae - snake eels							
Myrophis punctatus speckled worm eel	+	+		2, 3, 17, 18	Polychaetes, *Branchiostoma caribaeum*, sand crabs	Springer & Woodburn 1960, Reid 1954	Members of this family burrow in mud or sand, undersampled by most methods (Bohlke & Chaplin 1968)
Bascanichthys scuticaris - whip eels		+		3			
Ophichthus gomesi - shrimp eel		+		3, 17			
Clupeidae - herrings							
Brevoortia smithi - yellowfin sardine	+	+		2, 5, 17			
Brevoortia patronus - Gulf menhaden	+			12	38-48 mm: phytoplankton, zooplankton, plant fragments, detritus 85-103 mm: organic matter, silt, diatoms, foraminiferans, copepods	Darnell 1958	

Family and Species	Habitat Type			Reference	Diet	Diet Reference	Comments
	Tidal Stream	Estuarine Bay	Oceanic Bay				
Harengula pensacolae scaled sardine	+	+	+	2, 3, 8, 13	30 mm: planktonic copepods, zoea, nauplii, larval fish 64-96 mm: amphipods, harpacticoid copepods, isopods, mysids, chironomid larvae	Odum 1971	
Opisthonema oglinum - Atlantic thread herring	+	+	+	2, 3, 5, 13, 17	Copepods, polychaetes, shrimp, fishes, crab larvae, mysids	Odum 1971	
Sardinella anchovia Spanish sardine		+		17			
Engraulidae - anchovies							
Anchoa cubana - Cuban anchovy		+		2, 16	Ostracods, copepods	Springer & Woodburn 1960	
Anchoa hepsetus - striped anchovy	+	+		2, 3, 13, 16, 17	32-114 mm: copepods, isopods, mysids, caridean shrimp, small bivalves	Springer & Woodburn 1960	
Anchoa lamprotaenia - bigeye anchovy			+	5			
Anchoa mitchilli - bay anchovy	+	+	+	1, 2, 3, 5, 7, 8, 13, 16-18	<25 mm: microzooplankton 31-62 mm: amphipods, zooplankton, mysids, ostracods, plant detritus, copepods, small molluscs, chironomid larvae	Odum 1971	
Synodontidae - lizardfishes							
Synodus foetens - inshore lizardfish	+	+	+	1-3, 5, 8, 17, 18	Small fish, crabs, shrimp, polychaete worms	Odum 1971	
Catostomidae - suckers							
Erimyzon sucetta - lake chubsucker	+			6			A freshwater stray
Ictaluridae - freshwater catfish							
Ictalurus natalis - yellow bullhead	+			14			A freshwater stray
Noturus gyrinus - tadpole madtom	+			14			A freshwater stray
Arriidae - sea catfishes							
Arius felis - sea catfish	+	+	+	2, 3, 5, 7, 8, 13, 17	100 mm: copepods, zooplankton amphipods, mysids, chironomid larvae, isopods, small crabs 100-200 mm: benthic invertebrates 200-330 mm: crabs, amphipods, mysids, fishes, bark, crayfish, caridean and penaeid shrimp	Odum 1971	
Bagre marinus - gafftopsail catfish	+	+		2, 8, 17	262-445 mm: blue crabs, small fishes	Odum 1971	
Batrachoididae - toadfishes							
Opsanus beta - Gulf toadfish	+	+	+	1-3, 5, 7, 12, 13, 15, 17, 18	18-60 mm: amphipods, chironomid larvae, mysids, isopods, few fish >60 mm: caridean shrimp, xanthid crabs, snapping shrimp, mussels, fish, mangrove bark	Odum 1971	Salinities 10 o/oo > (Odum 1971)

Family and Species	Habitat Type			Reference	Diet	Diet Reference	Comments
	Tidal Stream	Estuarine Bay	Oceanic Bay				
Porichthys porosissimus Atlantic midshipman		+		3, 18			
Gobiesocidae - clingfishes							
Gobiesox strumosus skilletfish	+	+	+	2, 3, 5, 8	10-32 mm: amphipods, isopods, chironomid larvae	Odum 1971	
Ogcocephalidae - batfishes							
Ogcocephalus nasutus shortnose batfish		+	+	18	Small bivalves, gastropods, polychaetes	Reid 1954	
Ogcocephalus radiatus polka-dot batfish		+		2, 11, 17, 18			
Gadidae - codfishes							
Urophycis floridanus Southern hake	+			12	Amphipods, isopods, mysids, decapod shrimp, polychaetes, insect larvae, fishes (*Lagodon rhomboides*, *Paralichthys albigutta*)	Springer & Woodburn 1960	A species more common at more northerly latitudes
Ophidiidae - cusk-eels, brotulas							
Gunterichthys longipenis gold brotula		+		17			
Ogilbia cayorum key brotula		+	+	1, 3			
Ophidion holbrooki bank cusk-eel		+		3			
Exocoetidae - flyingfishes, halfbeaks							
Chriodorus atherinoides hardhead halfbeak			+	5			
Hyporhamphus unifasciatus halfbeak		+	+	2, 3, 5	juveniles: zooplankton including crab megalops, veligers, copepods 130-199 mm: epiphytic algae, detritus, seagrass	Carr & Adams 1973	
Belonidae - needlefishes							
Strongylura marina Atlantic needlefish	+	+		2, 7, 15	357-475 mm: small fishes, insects, shrimp, small amounts of vascular plant material and algae	Darnell 1958	
Strongylura notata redfin needlefish	+	+	+	2, 3, 5, 8, 13	In grassbeds - Juveniles: polychaete worms, cumaceans, fish Adults: fish, primarily atherinids	Brock 1975	
Strongylura timucu timucu	+	+	+	2, 3, 11	159-378 mm: anchovies, shrimp	Randall 1967	Primarily inshore species, freely enters freshwater (Randall 1967)
Tylosurus crocodilus - houndfish			+	11	250-1320 mm: fishes, shrimp	Randall 1967	Open water and inshore surface water inhabitant (Voss et al. 1969)

Family and Species	Habitat Type Tidal Stream	 Estuarine Bay	 Oceanic Bay	Reference	Diet	Diet Reference	Comments
Cyprinodontidae - killifishes							
Adinia xenica - diamond killifish	+			2, 8, 13-15	Plant detritus, diatoms, amphipods, harpacticoid copepods, insects	Odum 1971	
Cyprinodon variegatus sheepshead minnow	+	+	+	2, 7, 8, 13-15	Plant detritus, algae, nematodes, small crustaceans	Odum 1971	
Floridichthys carpio goldspotted killifish	+	+		2, 3, 8, 13	Amphipods, ostracods, isopods, copepods, chironomid larvae, nematodes, plant detritus, algae	Odum 1971	
Fundulus confluentus marsh killifish	+			2, 8, 13-15	Caridean shrimp, small fish, (*Gambusia affinis*), amphipods, isopods, adult & larval insects, copepods, mysids, ostracods, algal filaments	Odum 1971	
Fundulus chrysotus golden topminnow	+			14, 15			Rare in mangrove zone, headwater pools only
Fundulus grandis Gulf killifish	+			2, 8, 13-15	Amphipods, isopods, xanthid crabs, chironomid larvae, terrestrial insects, snails, algae, small fish (poeciliids)	Odum 1971	
Fundulus heteroclitus Mummichog	+			7	Small crustaceans (amphipods, isopods, ostracods, tanaids, copepods), detritus, polychaete worms, insects, snails, invertebrate eggs	Peterson & Peterson 1979	
Fundulus seminolis Seminole killifish	+			14-15			Primarily a freshwater form, headwater pools only
Jordanella floridae flagfish	+			13-15			Primarily freshwater, common in pools in headwater regions
Lucania goodei bluefin killifish	+			2, 8, 13-15	Small crustaceans (copepods, cladocerans, ostracods), insect larvae	Odum 1971	Headwater pools and channel
Lucania parva rainwater killifish	+	+	+	1-3, 5, 8, 13-15, 17	<20 mm: planktonic copepods 21-37 mm: amphipods, mysids, chironomid larvae, ostracods, molluscs, plant detritus	Odum 1971	
Rivulus marmoratus rivulus	+			3, 8, 13, 15			
Poeciliidae - livebearers							
Gambusia affinis mosquitofish	+			2, 3, 7, 13-15	A versatile feeder: amphipods, chironomid larvae, hydracarina, harpacticoid copepods, snails, ants, adult insects, polychaete worms, ostracods, mosquito pupae, algae	Odum 1971	
Gambusia rhizophorae mangrove gambusia	+			6, 9			Fresh and brackish water in *Rhizophora* swamps, northern Cuba, southeastern Florida

Family and Species	Habitat Type Tidal Stream	 Estuarine Bay	 Oceanic Bay	Reference	Diet	Diet Reference	Comments
Heterandria formosa least killifish	+			8, 14, 15	Chironomid larvae, harpacticoid and planktonic copepods, cladocerans, terrestrial insects, algae, diatoms	Odum 1971	
Poecilia latipinna sailfin molly	+		+	5, 7, 8, 13-15	Plant detritus, algae, diatoms	Odum 1971	
Atherinidae - silversides							
Allanetta harringtonensis reef silverside			+	5	39-60 mm: copepods, fish larvae, polychaete larvae	Randall 1967	
Membras martinica rough silverside		+	+	2, 5, 11	Small zooplankton crustaceans, juvenile & larval fishes, insects, detritus, snails	Peterson & Peterson 1979	
Menidia beryllina tidewater silverside	+	+	+	2, 3, 8, 11, 12, 13, 17, 18	Insects, copepods, chironomid larvae, mysids, amphipods	Odum 1971	
Syngnathidae - pipefishes, seahorses							
Corythoichthys albirostris whitenose pipefish			+	1, 11			
Hippocampus erectus lined seahorse		+	+	1, 2, 3, 11, 17			Associated with vegetated areas (Tabb & Manning 1961)
Hippocampus zosterae dwarf seahorse		+	+	1, 2, 3, 5, 11, 16, 17, 18			Intimately associated with unattached algae (Tabb & Manning 1961), or grassy areas (Springer & Woodburn 1960)
Micrognathus crinigerus fringed pipefish		+	+	1, 5, 10	52-82 mm: copepods, microcrustaceans	Reid 1954	
Syngnathus floridae dusky pipefish		+	+	1-3, 5, 11	Caridean shrimp, amphipods, tanaids, isopods	Brook 1975	
Syngnathus louisianae chain pipefish		+	+	1-3, 11, 16-18	Copepods, amphipods, small shrimp	Reid 1954	Inhabit grassy flats (Springer & Woodburn 1960)
Syngnathus scovelli Gulf pipefish	+	+	+	1-3, 5, 11, 16-18	Amphipods, isopods, tanaids, copepods, tiny caridean shrimp, gastropods (*Bittium*, *Mitrella*)	Brook 1975 Springer & Woodburn 1960 Reid 1954	
Syngnathus springeri bull pipefish		+		2, 17			
Syngnathus dunckeri Pugnose pipefish			+	11			Associated with vegetated areas (Tabb & Manning 1961)
Syngnathus pelagicus sargassum pipefish			+	1			
Centropomidae - snooks							
Centropomus parallelus fat snook	+			7			Family as a whole shows preference for estuarine mangrove habitat (Rivas 1962)
Centropomus pectinatus tarpon snook	+			7, 8, 13			

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Family and Species	Habitat Type			Reference	Diet	Diet Reference	Comments
	Tidal Stream	Estuarine Bay	Oceanic Bay				
Centropomus undecimalis snook	+	+	+	2, 5, 7, 8, 11, 13, 14	Juveniles: caridean shrimp, small cyprinodont fishes, gobies, mojarras Adults: fish, crabs, penaeid shrimp, crayfish, snapping shrimp	Odum 1971 Austin & Austin 1971	By far most abundant of three species (Rivas 1962)
Serranidae - sea basses							
Centropristis striata black seabass			+	11	Family in general carnivorous on fish, crustaceans	Randall 1967	
Diplectrum formosum sand perch		+	+	2, 3, 11, 16-18	Caridean & penaeid shrimp, copepods, crabs, fish	Reid 1954	
Epinephelus itajara jewfish	+	+	+	2, 5, 7, 8, 11, 13, 15	Juveniles: penaeid shrimp, xanthid crabs	Odum 1971	The most abundant of the seabasses in mangrove habitats
Epinephelus morio red grouper			+	11	228-340 mm: crustaceans, crabs, fishes	Randall 1967	
Epinephelus striatus Nassau grouper			+	4, 11	170-686 mm: fish, crabs, stomatopods, cephalopods, shrimp, spiny lobsters, gastropods, bivalves, isopods	Randall 1967	
Hypoplectrus puella barred hamlet			+	11	54-98 mm: snapping shrimp, crabs, fish, mysids, stomatopods, isopods	Randall 1967	
Mycteroperca microlepis gag		+	+	1, 2, 5, 11, 17, 18	71-100 mm: penaeid shrimp, fish	Reid 1954	
Centrarchidae - sunfishes							
Elassoma evergladei Everglades pygmy sunfish	+			14			Family is primarily freshwater, fish occasionally enter headwater area of mangrove-fringed stream
Lepomis auritus redbreast sunfish	+			14			
Lepomis gulosus warmouth	+			2, 13, 15	Shrimp (*Palaemonetes*), fish (*Gobiosoma bosci*, *Lepomis macrochirus*), detritus, *Vallisneria*, amphipods, xanthid crabs, blue crabs	Desselle et al. 1978	Diet from Lake Pontchartrain salinities 1.6-4.1 o/oo
Lepomis macrochirus bluegill	+			2, 15	Amphipods, blue crab (*Callinectes sapidus*), xanthid crabs, detritus, *Vallisneria*, clams (*Rangia cuneata*), sponge (*Ephydatia fluviatilis*), barnacles, insect larvae	Desselle et al. 1978	Diet from Lake Pontchartrain salinities 1.6-4.1 o/oo
Lepomis microlophus redear sunfish	+			2, 13-15	Chironomid larvae, amphipods, xanthid crabs, clam (*Rangia cuneata*), sponge (*Ephydatia fluviatilis*), detritus	Desselle et al. 1978	Diet from Lake Pontchartrain salinities 1.6-4.1 o/oo
Lepomis punctatus spotted sunfish	+			8, 14, 15	Cladocerans, small crabs, mysids, chironomids, amphipods, insects, molluscs, isopods, fish, algae	Odum 1971	Salinities < 15 o/oo (Odum 1971)

Family and Species	Habitat Type Tidal Stream	 Estuarine Bay	 Oceanic Bay	Reference	Diet	Diet Reference	Comments
Micropterus salmoides largemouth bass	+			13-15	Caridean shrimp, small blue crabs, crayfish, xanthid crabs, 25 species of fish, Vallisneria, Cladophora	Darnell 1958	
Apogonidae - cardinalfishes							
Astrapogon alutus bronze cardinalfish		+	+	1, 3			
Astrapogon stellatus conchfish			+	1			
Pomatomidae - bluefishes							
Pomatomus saltatrix bluefish			+	11	Young: mainly fishes (anchovies, silversides, killifishes, menhaden, shad, spotted seatrout), shrimp, crabs, other small crustaceans, annelids, snails	Peterson & Peterson 1979	
Rachycentridae - cobias							
Rachycentron canadum cobia		+	+	5, 7, 11	Fish, crabs	Randall 1967	
Echeneidae - remoras							
Echeneis neucratoides whitefin sharksucker	+	+	+	2, 11	Fish, isopods, other crustacea	Randall 1967	Members of this family attach to sharks and large bony fishes (Randall 1967)
Remora remora remora	+			7	58-175 mm: copepods, isopods, vertebrate muscle tissue, crab larvae, fish remains, crustaceans, amphipods	Randall 1967	
Carangidae - jacks, pompanos							
Caranx crysos - blue runner	+	+	+	2, 4, 5, 7, 11			Family of swift-swimming, carnivorous fishes, often running in schools, wide-ranging (Randall 1967)
Caranx hippos crevalle jack	+	+	+	2, 5, 7, 8, 11, 13	Fishes, crustaceans	Odum 1971	
Caranx ruber bar jack			+	4, 11	160-547 mm: fish, shrimp, mysids, stomatopods, gastropods	Randall 1967	
Chloroscombrus chrysurus Atlantic bumper		+	+	2, 11, 17, 18			
Oligoplites saurus leatherjacket	+	+	+	2, 3, 5, 8, 11, 13	Snapping shrimp, penaeid shrimp, larval anchovies, ladyfish, harpacticoid copepods	Tabb & Manning 1961	
Trachinotus carolinus Florida pompano			+	11	sardines (Harengula sp.), mole crabs (Hippa sp.), bivalves (Donax sp.)	Springer & Woodburn 1960	Common over mud bottoms (Randall 1967)
Trachinotus falcatus permit	+		+	7, 11	15-70 mm: mysids, shrimp, anchovies, silversides, crabs, snails	Carr & Adams 1973	More apt to occur over sandy bottoms than T. carolinus (Randall 1967)
Selene vomer lookdown	+	+	+	2, 3, 7, 11	Young: shrimp and other crustaceans, small molluscs	Peterson & Peterson 1979	

Family and Species	Habitat Type Tidal Stream	 Estuarine Bay	 Oceanic Bay	Reference	Diet	Diet Reference	Comments
Hemicaranx amblyrhynchus - bluntnose jack		+		17			
Caranx latus horse-eye jack	+			12	Predaceous on other fishes	Darnall 1958	Considered by Gunter (1956) to be euryhaline
Lutjanidae - snappers							
Lutjanus analis mutton snapper			+	1, 4, 11	204-620 mm: crabs, fish, gastropods, octopods, hermit crabs, penaeid shrimp, spiny lobster, stomatopods	Randall 1967	Commonly found over sand, sea-grass, rubble, coral reefs (Randall 1967)
Lutjanus apodus schoolmaster	+		+	1, 4, 5, 7, 11	Crustaceans (shrimp, snapping shrimp, blue crabs, xanthid crabs, grapsid crabs), fish	Nugent 1970	
Lutjanus griseus gray snapper	+	+	+	1-5, 7, 8, 11-13, 15-18	<50 mm: reside in grassbeds feeding on small crustaceans, insect larvae 95-254 mm: reside in mangrove creeks feeding on crustaceans (snapping shrimp, xanthid crabs, penaeid shrimp, crayfish, caridean shrimp), fish including gobies, anchovies, poeciliids, eels, killifishes	Odum 1971	By far the most abundant snapper in mangrove habitats
Lutjanus jocu dog snapper			+	1	190-630 mm: fish, crabs, octopods, spiny lobster, gastropods	Randall 1967	
Lutjanus synagris lane snapper	+	+	+	1, 2, 3, 5, 7, 11, 16-18	snapping shrimp, crabs, anchovies, annelids, molluscs	Stark & Schroeder 1970	Known from brackish water to depths of 220 fathoms (Randall 1967)
Gerreidae - mojarras							
Diapterus olisthostomus Irish pompano		+		2	110-116 mm: green algae (*Enteromorpha flexuosa*, *Cladophora*), *Ruppia maritima*, blue-green algae (*Lyngbe majuscula*)	Austin & Austin 1971	
Diapterus plumieri striped mojarra	+	+	+	2, 7, 8, 11-13, 15, 18	36-172 mm: mysids, amphipods, harpacticoid copepods, chironomid larvae, ostracods, bivalves, plant detritus	Odum 1971	A permanent resident (Odum 1971)
Eucinostomus argenteus spotfin mojarra	+	+	+	1-5, 7, 8, 11-13, 16-18	19-63 mm: amphipods, chironomids, harpacticoid copepods, ostracods, mysids, molluscs, plant detritus	Odum 1971	
Eucinostomus gula silver jenny	+	+	+	1-3, 5, 7, 8, 11-13, 16-18	19-70 mm: amphipods, chironomid larvae, harpacticoid copepods, molluscs, mysids, ostracods, plant detritus	Odum 1971	
Eucinostomus lefroyi mottled mojarra	+		+	10			
Gerres cinereus yellowfin mojarra	+		+	2, 7, 11	Crabs, bivalves, gastropods, polychaete worms, shrimp, ostracods	Randall 1967, Austin & Austin 1971	
Pomadasyidae - grunts					Family carnivorous though rarely piscivorous	Randall 1967	Most shelter on coral reef by day, feed on grassy flats by night (Randall 1967)

Family and Species	Habitat Type Tidal Stream	 Estuarine Bay	 Oceanic Bay	Reference	Diet	Diet Reference	Comments
Anisotremus virginicus porkfish			+	11	112-264 mm: brittle stars, crabs, shrimp, polychaetes, isopods, bivalves, stomatopods, gastropods	Randall 1967	
Haemulon aurolineatum tomtate			+	1, 4, 11	97-170 mm: shrimp & shrimp larvae, polychaetes, hermit crabs, amphipods, copepods, gastropods, bivalves	Randall 1967	
Haemulon carbonarium Caesar grunt			+	1	156-273 mm: crabs, gastropods, sea urchins, chitons, polychaetes, brittle stars, sipunculid worms, shrimp	Randall 1967	
Haemulon flavolineatum French grunt			+	4	113-228 mm: polychaetes, crabs, sipunculid worms, chitons, holothurians, isopods, shrimp, bivalves	Randall 1967	
Haemulon parrai sailor's choice	+		+	1, 7	Benthic invertebrates including shrimp, crabs, amphipods, gastropods, polychaete worms, bivalves	Randall 1967	
Haemulon plumieri white grunt		+	+	1, 2, 11, 18	130-279 mm: crabs, polychaete worms, sea urchins, sipunculid worms, gastropods, shrimp, brittle stars; juveniles: copepods, mysids	Randall 1967 Reid 1954	
Haemulon album margate	+			7	Benthic invertebrates including crabs, shrimp, polychaete worms, amphipods, copepods, snails, bivalves	Randall 1967	
Haemulon sciurus bluestriped grunt	+	+	+	1, 3, 5, 7, 11	Benthic invertebrates including crustaceans, molluscs, annelid worms	Randall 1967	
Orthopristis chrysoptera pigfish		+	+	1-3, 5, 11, 16-18	Juveniles: 16-30 mm: plankton including copepods, mysids, postlarval shrimp >30 mm: polychaetes, shrimp, amphipods	Carr & Adams 1973	Strong preference for vegetated substrate in bay areas (Weinstein et al. 1977)
Sparidae - porgies							
Archosargus probatocephalus sheepshead	+	+	+	2, 3, 5, 7, 8, 11-13, 17-18	<40 mm: in grassbeds - copepods, amphipods, chironomid larvae, mysids, algae, molluscs >40 mm: in mangrove creeks - mussels, false mussels, crabs, snapping shrimp, crayfish, hydrazoans, algae, plant detritus 32-85 mm: in Puerto Rico mangroves - 100% blue-green algae (*Lyngbya mojuscula*)	Odum 1971 Austin & Austin 1971	
Archosargus rhomboidalis sea bream			+	5, 11	105-220 mm: seagrasses *Cymodocea* & *Thalassia*, algae, crabs, gastropods, invertebrate eggs, bivalves	Randall 1967	Usually seen in mangrove sloughs, rare on reefs (Randall 1967)
Calamus arctifrons grass porgy		+	+	11, 17	Copepods, amphipods, mysids, shrimp, bivalves, gastropods (*Mitrella*, *Bittium*), polychaetes	Reid 1954	Associated with grassy flats (Tabb & Manning 1961)
Calamus calamus saucereye porgy			+	1	190-250 mm: polychaetes, brittle stars, bivalves, hermit crabs, sea urchins, gastropods, chitons	Randall 1967	

Family and Species	Habitat Type			Reference	Diet	Diet Reference	Comments
	Tidal Stream	Estuarine Bay	Oceanic Bay				
Lagodon rhomboides pinfish	+	+	+	1-3, 5, 7, 8, 11, 12, 16-18	In mangrove creek - scorched mussel, mysids, amphipods, false mussel In Whitewater Bay - 100% plant material	Odum 1971 Reid 1954	Strong preference for vegetated substrate in bay areas (Weinstein et al. 1977)
Sciaenidae - drums							
Bairdiella batabana blue croaker		+	+	3, 11			
Bairdiella chrysura silver perch	+	+	+	1-3, 8, 11-13, 16-18	Larvae: copepods, larval fish (*Menidia beryllina*) 127-181 mm: fish (*Anchoa mitchilli*), mysids	Odum 1971	
Cynoscion arenarius sand seatrout	+	+		2, 12, 17, 18	Mostly fish, caridean shrimp, mysids, amphipods, crab zoea	Springer & Woodburn 1960	
Cynoscion nebulosus spotted seatrout	+	+	+	1-3, 5, 7, 8, 11-13, 15, 17, 18	<50 mm: copepods, planktonic crustacea 50-275 mm: fish (*Mugil cephalus*, *Lagodon rhomboides*, *Eucinostomus gula*, *E. argenteus*, *Cyprinodon variegatus*, *Gobiosoma robustum*, *Anchoa mitchilli*)	Odum 1971	
Leiostomus xanthurus spot	+	+		2, 7, 12, 17-18	<40 mm: planktonic organisms >40 mm: filamentous algae, desmids, forams, amphipods, mysids, copepods, ostracods, isopods, chuetognaths, bivalves, snails, polychaete worms	Springer & Woodburn 1960	
Menticirrhus americanus Southern kingfish	+	+	+	2, 11-12, 17-18	Fish, benthic crustaceans	Springer & Woodburn 1960	
Menticirrhus littoralis Gulf kingfish		+	+	2, 11	Polychaetes, bivalves (*Donax*), sand crab (*Emerita*), razor clams	Springer & Woodburn 1960	Most common off sandy beaches (Springer & Woodburn 1960)
Micropogon undulatus Atlantic croaker	+		+	11, 12	Juveniles: copepods, mysids, caridean shrimp, polychaete worms, insect larvae, isopods, small bivalves	Springer & Woodburn 1960	
Pogonias cromis black drum	+	+	+	2, 7, 11, 12, 15	<100 mm: molluscs, xanthid crabs >100 mm: bivalves, amphipods, blue crabs, penaeid shrimp, caridean shrimp	Darnell 1958	
Sciaenops ocellata red drum	+	+	+	2, 3, 5, 8, 11-13, 15, 17	<10 mm: planktonic organisms (copepods, crab zoea, larval fish) 34-42 mm: mysids, amphipods, caridean shrimp >50 mm: xanthid & portunid crabs, penaeid shrimp, small fish 308-403 mm: xanthid crabs	Odum 1971	
Equetus acuminatus high-hat			+	11	68-152 mm: shrimp & shrimp larvae, isopods, stomatopod larvae, copepods, amphipods	Randall 1967	Characteristic of coral reefs (Randall 1967)

Family and Species	Habitat Type			Reference	Diet	Diet Reference	Comments
	Tidal Stream	Estuarine Bay	Oceanic Bay				
Ephippidae - spadefishes							
Chaetodipterus faber Atlantic spadefish		+	+	2, 3, 5, 11, 16-18	Worms, crustaceans, debris	Darnell 1961	Juveniles (7-12 mm) inhabit very shallow nearshore sandy beaches. Bear a deceptive resemblance to infertile red mangrove seed pods (Breder 1946)
Pomacentridae - damselfishes							Characteristic family of coral reefs (Randall 1967)
Abudefduf saxatilis sergeant major			+	5	101-135 mm: copepods, algae, fish eggs, fish, shrimp larvae, polychaetes	Randall 1967	A habitat generalist: reefs, grassbeds, rock piles, wharfs (Bohlke & Chaplin 1968)
Labridae - wrasses							
Halichoeres bivittatus slippery dick			+	5	67-153 mm: crabs, sea urchins, polychaetes, gastropods, brittle stars, bivalves, shrimp, fish, hermit crabs	Randall 1967	Shallow water patch reefs, sand bottoms, grassbeds (Randall 1967)
Scaridae - parrotfishes							
Nicholsina usta emerald parrotfish		+	+	1, 2, 11, 18	Family herbivorous, feeding primarily on algae growing on hard substrates, secondarily on seagrasses	Randall 1967	Family characteristic of coral reefs, ranging into grassbeds
Scarus coeruleus blue parrotfish			+	1			
Scarus croicensis striped parrotfish			+	4			
Sparisoma chrysopterum redtail parrotfish			+	11			
Sparisoma rubripinne redfin parrotfish			+	1			Requires near marine salinities (Tabb & Manning 1961)
Sparisoma viride stoplight parrotfish			+	11			
Mugilidae - mullets							
Mugil cephalus striped mullet	+	+	+	2, 3, 5, 7, 8, 11-13, 15	Inorganic sediments, fine detritus, micro-algae	Odum 1971	
Mugil curema white mullet	+	+	+	2, 5, 7, 11-12	25-73 mm: plant detritus, blue-green algae (*Lyngbya majuscula*)	Austin & Austin 1971	
Mugil trichodon fantail mullet	+	+	+	2, 7, 11, 12			
Sphyraenidae - barracudas *Sphyraena barracuda* great barracuda	+	+	+	1-5, 7, 8, 11, 13	135-369 mm: fish (*Eucinostomus gula*, *Menidia beryllina*, *Archosargus probatocephalus*)	Odum 1971	Salinities >10 o/oo (Odum 1971)
Opistognathidae - jawfishes							
Opistognathus maxillosus mottled jawfish			+	1	53-110 mm: shrimp, isopods, fishes, polychaetes, mysids, copepods	Randall 1967	Family lives in burrows in sediment, often in vicinity of reefs (Randall 1967)

Family and Species	Habitat Type Tidal Stream	 Estuarine Bay	 Oceanic Bay	Reference	Diet	Diet Reference	Comments
Clinidae - clinids				5	Family appears to be carnivorous on benthic invertebrates	Randall 1967	Inshore on rock, coral or rubble substrates (Randall 1967)
Chaenopsis ocellata bluethroat pikeblenny			+				
Paraclinus marmoratus marbled blenny			+	1, 5, 11			
Paraclinus fasciatus banded blenny			+	1			
Stathmonotus hemphilli blackbelly blenny			+	1			
Blenniidae - combtooth blennies							
Chasmodes saburrae Florida blenny		+	+	1-3, 11, 17, 18	21-25 mm: amphipods 25-60 mm: amphipods, detritus, polychaetes, snails	Carr & Adams 1973	Common brackish water blenny (Tabb & Manning 1961)
Blennius marmoreus seaweed blenny			+	5	Algae, organic detritus, brittle stars, polychaetes, hydroids	Randall 1967	
Blennius nicholsi highfin blenny		+		2			
Callionymidae - dragonets							
Callionymus pauciradiatus spotted dragonet			+	1, 5, 11			
Eleotridae - sleepers							
Dormitator maculatus fat sleeper	+			13, 15			Freshwater and low salinity areas (Darnell 1961)
Gobiidae - gobies							
Bathygobius soporator frillfin goby	+	+	+	2, 3, 8, 11, 17	Caridean shrimp, chironomid larvae, amphipods	Odum 1971	
Gobionellus hastatus sharptail goby	+			12	Filamentous algae (*Enteromorpha*), ostracods, copepods, insect larvae	Springer & Woodburn 1960	
Gobionellus shufeldti freshwater goby	+	+		2, 17, 18			
Gobionellus smaragdus emerald goby	+	+	+	3, 8, 10, 11, 15			
Gobiosoma bosci naked goby	+	+		2, 12	Small crustaceans including amphipods, annelids, fish, fish eggs	Peterson & Peterson 1979	
Gobiosoma longipala twoscale goby		+		17			
Gobiosoma macrodon tiger goby			+	1			
Gobiosoma robustum code goby	+	+	+	1-3, 5, 8, 11, 16-18	Amphipods, mysids, chironomid larvae	Odum 1971	
Lophogobius cyprinoides crested goby	+	+	+	1-3, 7, 8, 13	A versatile feeder: amphipods, mangrove detritus, filamentous algae, mysids, caridean & penaeid shrimp, polychaete worms, ostracods, bivalves, chironomid larvae, harpacticoid copepods, isopods, xanthid crabs, snails	Odum 1971	

Family and Species	Habitat Type Tidal Stream	 Estuarine Bay	 Oceanic Bay	Reference	Diet	Diet Reference	Comments
Microgobius gulosus clown goby	+	+		2, 5, 8, 11-13, 15, 17, 18	Amphipods, copepods, chironomid larvae	Odum 1971	
Microgobius microlepis banner goby			+	5	Planktonic organisms	Birdsong 1981	
Microgobius thalassinus green goby	+	+		2, 3, 12	Small crustaceans including amphipods, other invertebrates	Peterson & Peterson 1979	
Scombridae - mackerels, tunas							
Scomberomorus maculatus Spanish mackerel	+	+	+	2, 11, 12, 15	Adults feeding on penaeid shrimp migrating from tidal stream	Tabb & Manning 1961	
Scomberomorus cavalla king mackerel			+	11	350-1022 mm: fish	Randall 1967	
Scorpaenidae - scorpionfishes							
Scorpaena brasiliensis barbfish	+		+	7, 11	Shrimp, other crustaceans, fish	Randall 1967	
Scorpaena grandicornis plumed scorpionfish			+	1	37-102 mm: shrimp, fish, unidentified crustaceans	Randall 1967	Most often found in seagrass
Triglidae - searobins							
Prionotus salmonicolor blackwing searobin			+	5			
Prionotus scitulus leopard searobin	+	+	+	1-3, 11, 16-18	Small molluscs, shrimp, crabs fish, small crustaceans (ostracods, cumaceans)	Peterson & Peterson 1979	
Prionotus tribulus bighead searobin	+	+	+	1-3, 11-13, 17, 18	Shrimp, crabs, fishes, amphipods, copepods, annelids, bivalves, sea urchins	Peterson & Peterson 1979	
Bothidae - lefteye flounders							
Bothus ocellatus eyed flounder			+	1, 11	68-130 mm: fish, crabs, shrimp, amphipods	Randall 1967	
Citharichthys macrops spotted whiff			+	1			
Citharichthys spilopterus bay whiff		+	+	1, 17, 18	Mainly mysids, also shrimp, crabs, copepods, amphipods, fishes, annelids	Peterson & Peterson 1979	Recorded from salinity range 2.5-36.7 o/oo (Darnell 1961)
Etropus crossotus fringed flounder		+	+	3, 11, 16	Calanoid copepods, cumaceans, amphipods, mysids, shrimp, crabs, isopods, annelids, molluscs, fishes	Peterson & Peterson 1979	
Paralichthys albigutta Gulf flounder	+	+	+	1-3, 7, 11, 12, 17, 18	<45 mm: small crustaceans, including amphipods, small fish >45 mm: fish (pigfish, pinfish, lizardfish, bay anchovy, labrids), crustaceans	Springer & Woodburn 1960; Reid 1954	
Paralichthys lethostigma - Southern flounder		+		2	Mainly fishes (mullet, menhaden, shad, anchovies, pinfish, mojarras, croakers), crabs, mysids, molluscs, penaeid shrimp, amphipods	Peterson & Peterson 1979	

Family and Species	Habitat Type Tidal Stream	Estuarine Bay	Oceanic Bay	Reference	Diet	Diet Reference	Comments
Syacium papillosum dusky flounder			+	1			
Soleidae - soles							
Achirus lineatus lined sole	+	+	+	1-3, 5, 8, 11-13, 17-18	32-74 mm: chironomid larvae, polychaete worms, foraminiferans	Odum 1971	
Trinectes inscriptus scrawled sole			+	1			
Trinectes maculatus hogchoker	+	+	+	2, 3, 8, 11-13, 17, 18	14-110 mm: amphipods, mysids	Odum 1971	
Cynoglossidae - tonguefishes							
Symphurus plagiusa blackcheek tonguefish	+	+	+	1, 3, 11, 12, 16-18	35-102 mm: polychaete worms, ostracods, portunid crabs, Ruppia and Halodule plant tips	Austin & Austin 1971	
Balistidae - triggerfishes & filefishes							
Aluterus schoepfi orange filefish			+	1, 11	Seagrasses, algae, hermit crabs, gastropods	Randall 1967	Associated with grassbeds, sponge/sea fan habitats (Randall 1967; Voss et al. 1969)
Balistes vetula queen triggerfish			+	11	130-480 mm: sea urchins, crabs, bivalves, brittle stars, polychaetes, hermit crabs, gastropods, algae	Randall 1967	Solitary reef fish ranging into grassbeds
Monacanthus ciliatus fringed filefish		+	+	1, 11, 17	47-97 mm: Algae, organic detritus, seagrass, copepods, shrimp & shrimp larvae, amphipods, tanaids, polychaetes, molluscs	Randall, 1967 Springer & Woodburn 1960	Closely associated with vegetated areas (Tabb & Manning 1961)
Monacanthus hispidus planehead filefish		+	+	1-3, 11, 16-18	Detritus, bryozoans, annelids, harpacticoid copepods, amphipods, hermit crabs, molluscs, algae, sea urchins	Peterson & Peterson 1979	Associated with vegetated areas (Tabb & Manning 1961)
Balistes capriscus gray triggerfish	+			7			
Ostraciidae - boxfishes							
Lactophrys quadracornis scrawled cowfish	+	+	+	1. 2, 5, 7, 11, 16-18	Vegetation, algae, bivalves	Reid 1954	Young mimic seagrass blades (Bohlke & Chaplin 1968)
Lactophrys trigonus trunkfish			+	1, 4, 11	109-395 mm: crabs, bivalves, polychaetes, sea urchins, algae, seagrass, gastropods, amphipods	Randall 1967	Primarily a resident of seagrass (Randall 1967)
Lactophrys triqueter smooth trunkfish			+	1	93-250 mm: polychaetes, sipunculid worms, crabs, shrimp, gastropods, hermit crabs, sea urchins, bivalves	Randall 1967	Primarily a reef species (Randall 1967)
Tetraodontidae - puffers							
Sphoeroides nephelus southern puffer	+	+	+	1-3, 5, 11, 16-18	Juveniles: detritus, fecal pellets, zooplankton, polychaetes, gastropods, crabs, shrimp Adults: small crabs, bivalves	Carr & Adams 1973	

Family and Species	Habitat Type Tidal Stream	 Estuarine Bay	 Oceanic Bay	Reference	Diet	Diet Reference	Comments
Sphoeroides spengleri bandtail puffer	+		+	1, 7, 11	Crabs, bivalves, snails, polychaetes, amphipods, shrimp	Randall 1967	Inhabits sea-grass, reef, rubble, mangroves (Randall 1967; Voss et al. 1969)
Sphoeroides testudineus checkered puffer	+		+	1, 7	85-92 mm: portunid megalops larvae, gastropods	Austin & Austin 1971	
Diodontidae - porcupine-fishes							
Chilomycterus antennatus bridled burrfish			+	11	Gastropods, hermit crabs, isopods, crabs, shrimp	Randall 1967	Reefs and grass-beds (Voss et al. 1969)
Chilomycterus antillarum web burrfish		+		2			
Chilomycterus schoepfi striped burrfish		+	+	1-3, 5, 11, 16-18	Gastropods, barnacles, crabs, amphipods	Springer & Woodburn 1960	Associated with grassbeds (Voss et al. 1969) Salinities >25 o/oo (Springer & Woodburn 1960)

Reference Numbers Key

1. Bader & Roessler 1971
2. Carter et al. 1973
3. Clark 1970
4. Holm 1977
5. Hudson et al. 1970
6. Kushlan & Lodge 1974
7. Nugent 1970
8. Odum 1971
9. Rivas 1969
10. Seaman et al. 1973
11. Schmidt 1979
12. Springer & Woodburn 1960
13. Tabb 1966
14. Tabb, Dubrow & Manning 1962
15. Tabb & Manning 1961
16. Weinstein et al. 1977
17. Yokel 1975a
18. Yokel 1975b

APPENDIX C. Amphibians and reptiles recorded from south Florida mangrove swamps.

AMPHIBIANS AND REPTILES OF FLORIDA'S MANGROVES

Species	Status	Food Habits
Mud Turtle (*Kinosternon subrubrum*)	Abundant	Insects, crustaceans, mollusks
Striped Mud Turtle (*Kinosternon bauri*)	Common	Algae, snails, dead fish
Ornate Diamondback Terrapin (*Malaclemys terrapin macrospilota* and *M.t. rhizophorarum*)	Uncommon	*Littorina*, *Melampus*, *Uca*, *Anomalocardia*
Florida Red-bellied Turtle (*Chrysemys nelsoni*)	Rare - Uncommon	*Sagittaria*, *Lemna*, *Naias*
Chicken Turtle (*Deirochelys reticularia*)	Uncommon	Crayfish, insects, Nuphar
Green Turtle (*Chelonia mydas*)	Uncommon	Mangrove roots and leaves, seagrasses
Hawksbill (*Eretmochelys imbricata*)	Rare	*Rhizophora*: fruits, leaves wood, bark
Loggerhead (*Caretta caretta*)	Common	Crabs, jellyfish, tunicates
Atlantic Ridley (*Lepidochelys kempii*)	Uncommon	Snails, crabs, clams
Florida Softshell (*Trionyx ferox*)	Common	Snails, crayfish, mussels, frogs, fish, waterfowl
Green Anole (*Anolis carolinensis*)	Common	Insects
Cuban Brown Anole (*Anolis sagrei*)	Common	Insects
Bahaman Bank Anole (*Anolis distichus*)	Uncommon	Insects
Green Water Snake (*Nerodia cyclopion*)	Common	Fish
Mangrove Water Snake (*Nerodia fasciata compressicauda*)	Common	Fish, invertebrates

AMPHIBIANS AND REPTILES OF FLORIDA'S MANGROVES (concluded)

Species	Status	Food Habits
Striped Swamp Snake (Liodytes alleni)	Uncommon	Crayfish, sirens, frogs
Eastern Indigo Snake (Drymarchon corais)	Uncommon	Small mammals, birds, frogs
Rat Snake (Elaphe obsoleta)	Uncommon	Small mammals, birds
Eastern Cottonmouth (Agkistrodon piscivorus)	Uncommon	Fish, frogs, snakes, birds, small mammals
American Alligator (Alligator mississippiensis)	Common	Fish, waterbirds
American Crocodile (Crocodylus acutus)	Rare	Fish, waterbirds
Giant Toad (Bufo marinus)	Common	Invertebrates
Squirrel Treefrog (Hyla squirella)	Abundant	Insects
Cuban Treefrog (Hyla septentrionalis)	Common	Insects, frogs, toads, lizards

References: Carr and Goin 1955; Ernst & Barbour 1972; Mahmuud 1965; L. Narcisse, R.N. "Ding" Darling Fed. Wildlife Refuge, Sanibell Is., Fla.; personal communication (1981).

APPENDIX D. Avifauna of south Florida mangrove swamps.

WADING BIRDS

Common Name (Latin name)	Abundance	Season of Occurrence[a]	Nesting[a]	Food Habits	References
Great Egret (*Casmerodius albus*)	Common	Yr	Y	Fish	Howell 1932 Kushlan & White 1977a
Snowy Egret (*Egretta thula*)	Common	Yr	Y	Fish	Howell 1932 Kushlan & White 1977a Ffrench 1966
Cattle Egret (*Bubulcus ibis*)	Common	Yr	Y	Fish	Howell 1932 Kushlan & White 1977a
Great White Heron (*Ardea herodias occidentalis*)	Rare	Yr	Y	Fish	Howell 1932 Kushlan & White 1977a
Great Blue Heron (*Ardea herodias*)	Common	Yr	Y	Fish	Howell 1932 Kushlan & White 1977a
Reddish Egret (*Dichromanassa rufescens*)	Uncommon	Yr	Y	Fish	Howell 1932 Kushlan & White 1977a
Louisiana Heron (*Hydranassa tricolor*)	Common	Yr	Y	Fish	Kushlan & White 1977a Maxwell & Kale 1977 Girard & Taylor 1979
Little Blue Heron (*Florida caerulea*)	Common	Yr	Y	Fish	Kushlan & White 1977a Maxwell & Kale 1977 Girard & Taylor 1979
Green Heron (*Butorides striatus*)	Common	Yr	Y	Fish	Robertson & Kushlan 1974 Maxwell & Kale 1977 Girard & Taylor 1979
Black-crowned Night Heron (*Nycticorax nycticorax*)	Common	Yr	Y	Fish, crustaceans, frogs, mice	Ffrench 1966 Maxwell & Kale 1977 Girard & Taylor 1979
Yellow-crowned Night Heron (*Nyctanassa violacea*)	Common	Yr	Y	Fish, crayfish, crabs	Ffrench 1966 Girard & Taylor 1979
Least Bittern (*Ixobrychus exilis*)	Uncommon	Yr	Y	Fish	Ffrench 1966
American Bittern (*Botaurus lentiginosus*)	Uncommon	W,T	Y	Crayfish, frogs, small fishes	Narcisse, pers. comm.[b]
Wood Stork (*Mycteria americana*)	Common (locally abundant)	Yr	Y	Fish	Kahl 1964 Ogden et al. 1976 Kushlan 1979
Glossy Ibis (*Plegadis falcinellus*	Uncommon	Yr	Y	Fish	Bacon 1970 Howell 1932
White Ibis (*Eudocimus albus*)	Abundant	Yr	Y	Fish, crabs (*Uca*)	Kushlan 1979 Kushlan & Kushlan 1975 Girard & Taylor 1979
Roseate Spoonbill (*Ajaia ajaja*)	Rare to Uncommon	Yr	Y	Shrimp, fish, aquatic vegetation	Kushlan & White 1977a Howell 1932
Sandhill crane (*Grus canadensis*)	Rare	Yr		Roots, rhizomes of *Cyperus* & *Sagittaria*	Ogden 1969 Howell 1932
Limpkin (*Aramus guarauna*)	Rare	Yr	Y	Snails (*Pomacea*)	Howell 1932 Bacon 1970

PROBING SHORE BIRDS

Common Name (Latin name)	Abundance	Season of Occurrence[a]	Nesting[a]	Food Habits	References
King Rail (*Rallus elgans*)	Common	Yr		Beetles, grasshoppers, aquatic bugs	Narcise, pers. comm. Martin et al. 1951
Clapper Rail (*Rallus longirostris*)	Uncommon-common	Yr	Y	Crabs, shrimp	Howell 1932 Ffrench 1966 Bacon 1970
Virginia Rail (*Rallus limicola*)	Rare	W		Beetles, snails, spiders	Marcisse, pers. comm. Martin et al. 1951
Sora (*Porzana carolina*)	Uncommon to locally abundant	W		Insects, seeds of emergent aquatic plants	Howell 1932 Bacon 1970
Black Rail (*Laterallus jamaicensis*)	Rare	W		Beetles, snails	Narcisse, pers. comm.
Semipalmated Plover (*Charadrius semipalmatus*)	Locally common	W,T		Crustaceans, mollusks	Ffrench 1966 Bacon 1970 Baker & Baker 1973
Wilson's Plover (*Charadrius wilsonia*)	Locally common	W,T		Crabs, shrimp, crayfish	Howell 1932 Bacon 1970
Black-bellied Plover (*Pluvialis squatarola*)	Common	W		Crabs, mollusks	Howell 1932 Bacon 1970 Ffrench 1966
Ruddy Turnstone (*Arenaria interpres*)	Common	W		Insects, crustaceans, mollusks	Ogden 1969 Howell 1932
Common Snipe (*Capella gallinago*)	Uncommon	W,T		Mollusks, insects, worms	Howell 1932 Bacon 1970
Long-billed Curlew (*Numenius americanus*)	Rare-uncommon	W,T		Crustaceans, insects	Ogden 1969
Whimbrel (*Numenius phaeopus*)	Uncommon	W		Mollusks, crustaceans, worms, insects	Ogden 1968 Howell 1932
Spotted Sandpiper (*Actitis macularia*)	Abundant	W,T		Mollusks, crustaceans	Ffrench 1966 Bacon 1970 Russel 1980
Solitary Sandpiper (*Tringa solitaria*)	Common	W,T		Crustaceans, aquatic insects, small frogs	Howell 1932 Bacon 1970
Willet (*Catoptrophorus semipalmatus*)	Common	Yr	Y	Crabs, crayfishes, killifishes	Howell 1932 Bacon 1970
Greater Yellowlegs (*Tringa melanoleucas*)	Common	W,T		Fishes, crabs, crustaceans	Howell 1932 Ffrench 1966 Bacon 1970
Lesser Yellowlegs (*Tringa flavipes*)	Common	W,T		Snails, mollusks, crabs	Ffrench 1966 Bacon 1970 Baker & Baker 1973
Red Knot (*Calidris canutus*)	Uncommon	W,T		Marine worms, crustaceans	Howell 1932 Ogden 1964
Dunlin (*Calidris alpina*)	Common	W		Marine worms, mollusks	Ogden 1964 Baker & Baker 1973
White-rumped Sandpiper (*Calidris fuscicollis*)	Rare	T		Chironomids, snails	Howell 1932 Bacon 1970

PROBING SHOREBIRDS (concluded)

Common Name (Latin name)	Abundance	Season of Occurrence[a]	Nesting[a]	Food Habits	References
Least Sandpiper (*Calidris minutilla*)	Common	W,T		Pupae of beetles and flies	Bacon 1970 Baker & Baker 1973
Short-billed Dowitcher (*Limnodromus griseus*)	Common	W,T		Mollusks, crustaceans	Bacon 1970 Baker & Baker 1973
Stilt Sandpiper (*Micropalama himantopus*)	Rare-uncommon	W,T		Chironomids	Howell 1932 Bacon 1970
Semipalmated Sandpiper (*Calidris pusilla*)	Common-abundant	W,T		Mollusks, insects	Bacon 1970 Baker & Baker 1973
Western Sandpiper (*Calidris mauri*)	Common-abundant	W,T		Chironomids	Howell 1932 Bacon 1970
Marbled Godwit (*Limosa fedoa*)	Rare-common	W		Crustaceans, mollusks, seeds of emergent aquatic plants	Howell 1932
American Avocet (*Recurvirostra americana*)	Uncommon	W,T		Marine worms, aquatic insects	Ogden 1969
Black-necked Stilt (*Himantopus mexicanus*)	Common	S		Aquatic beetles	Howell 1932 Bacon 1970

SURFACE AND DIVING BIRDS

Common Name (Latin name)	Abundance	Season of Occurrence[a]	Nesting[a]	Food Habits	References
Common Loon (*Gavia immer*)	Occasional	W		Fish, crabs, mollusks	Narcisse, pers. comm.
Horned Grebe (*Podiceps auritus*)	Uncommon	W		Fish, aquatic insects, mollusks	Ogden 1969
Pied-billed Grebe (*Podilymbus podiceps*)	Uncommon-common	Yr		Crayfish, fish, mollusks	Narcisse, pers. comm.
White Pelican (*Pelecanus erythrorhynchos*)	Rare Common	S W		Fish	Narcisse, pers. comm.
Brown Pelican (*Pelecanus occidentalis*)	Common	Yr	Y	Fish	Pfrench 1966 Bacon 1970
Double-crested cormorant (*Phalacrocorax auritus*)	Common	Yr	Y	Fish	Kushlan & White 1977a
Anhinga (*Anhinga anhinga*)	Common	Yr	Y	Fish	Pfrench 1966
Fulvous Whistling Duck (*Dendrocygna bicolor*)	Uncommon	W			Ogden 1969 Smith, pers. obs.
Mallard (*Anas platyrhynchos*)	Uncommon	W,T		Widgeon grass	Ogden 1969 Kushlan et al., in prep.
Black Duck (*Anas rubripes*)	Rare	W,T		Mollusks, crustaceans, widgeon grass	Ogden 1969
Mottled Duck (*Anas fulvigula*)	Uncommon	Yr	Y	*Polygonum*, snails, *Ruppia*	LaHunt & Cornwell 1970 Kushlan et al., in prep.
Gadwall (*Anas strepera*)	Uncommon	W,T		*Ruppia*, *Zostera*, mollusks	Ogden 1969
Pintail (*Anas acuta*)	Abundant	W,T		*Saggitaria*, mollusks, *Cyperus*	Narcisse, pers. comm. Kushlan et al., in prep.
Green-winged Teal (*Anas crecca carolinensis*)	Abundant	W,T		*Ruppia*, *Zostera*, aquatic insects	Narcisse, pers. comm. Kushlan et al., in prep.
Blue-winged Teal (*Anas discors*)	Abundant	Yr		*Cyperus*, snails, insects, crustaceans	Narcisse, pers. comm. Pfrench 1966
American Wigeon (*Anas americana*)	Common	W,T		*Ruppia*, *Zostera*, mollusks	Narcisse, pers. comm. Kushlan et al., in prep.
Northern Shoveler (*Anas clypeata*)	Common	W,T		mollusks, aquatic insects, *Ruppia*, *Zostera*	Narcisse, pers. comm.
Wood Duck (*Aix sponsa*)	Rare	W		Nuts, seeds	Ogden 1969
Redhead (*Aythya americana*)	Rare	W		Snails, clams, aquatic insects, *Ruppia*, *Zostera*	Ogden 1969
Ring-necked Duck (*Aythya collaris*)	Abundant	W		*Polygonum*, *Ruppia*, crayfish, snails	Ogden 1969 Kushlan et al., in prep.
Canvasback (*Aythya valisineria*)	Uncommon	W		*Vallisneria*, *Ruppia*, *Zostera*	Ogden 1969 Kushlan et al., in prep.

SURFACE AND DIVING BIRDS (concluded)

Common Name (Latin name)	Abundance	Season of Occurrence[a]	Nesting[a]	Food Habits	References
Lesser Scaup (*Aythya affinis*)	Common-abundant	W		Mollusks, *Ruppia*	Narcisse, pers. comm. Ogden 1969 Kushlan et al., in prep.
Bufflehead (*Bucephala albeola*)	Rare	W		Gastropods, crabs, crustaceans	Ogden 1969 Kushlan et al., in prep.
Ruddy Duck (*Oxyura jamaicensis*)	Common	W		*Potamogeton*, *Najas*, *Zostera*, *Ruppia*, mollusks	Ogden 1969 Kushlan et al., in prep.
Hooded Merganser (*Lophodytes cucullatus*)	Rare--uncommon	W		Fish	Ogden 1969
Red-breasted Merganser (*Mergus serrator*)	Common	W,T		Fish	Narcisse, pers. comm.
Purple Gallinule (*Porphyrula martinica*)	Rare	Yr	Y	Aquatic insects, mollusks, *Eleocharis*, *Paspalum*	Narcisse, pers. comm. Ffrench 1966
Common Gallinule (*Gallinula chloropus*)	Common	Yr	Y	Seeds, aquatic insects	Narcisse, pers. comm. Ffrench 1966
American Coot (*Fulica americana*)	Abundant	W,T		*Ruppia*, *Najas*, *Potamogeton*, aquatic insects	Narcisse, pers. comm.

AERIALLY SEARCHING

Common Name (Latin name)	Abundance	Season of Occurrence[a]	Nesting[a]	Food Habits	References
Herring Gull (*Larus argentatus*)	Uncommon	W		Fish, mollusks, crustaceans	Narcisse, pers. comm. Ogden 1969
Ring-billed Gull (*Larus delawarensis*)	Common	W,T		Fish, insects, mollusks	Narcisse, pers. comm. Ogden 1969
Laughing Gull (*Larus atricilla*)	Common	Yr		Fish, shrimp, crabs	Narcisse, pers. comm. Ogden 1969
Bonaparte's Gull (*Larus philadelphia*)	Uncommon	W		Fish, insects	Ogden 1969
Gull-billed Tern (*Gelochelidon nilotica*)	Uncommon	Yr		Mayflies, dragonflies	Ogden 1969
Forster's Tern (*Sterna fosteri*)	Uncommon-common	W		Fish	Narcisse, pers. comm. Ogden 1969
Common Tern (*Sterna hirundo*)	Uncommon	W		Fish	Ogden 1969
Least Tern (*Sterna albifrons*)	Common	S		Fish	Narcisse, pers. comm. Ogden 1969
Royal Tern (*Thalasseus maxima*)	Common	W,T		Fish	Ogden 1969
Sandwich Tern (*Sterna sandvicensis*)	Uncommon	Yr		Fish	Narcisse, pers. comm. Ogden 1969
Caspian Tern (*Sterna caspia*)	Uncommon	W		Fish	Ogden 1969
Black Skimmer (*Rynchops nigra*)	Common	Yr		Fish	Ogden 1969
Belted Kingfisher (*Megaceryle alcyon*)	Common	Yr		Fish	Narcisse, pers. comm.
Fish Crow (*Corvus ossifragus*)	Common	Yr	Y	Fish	Narcisse, pers. comm.

BIRDS OF PREY

Common Name (Latin name)	Abundance	Season of Occurrence[a]	Nesting[a]	Food Habits	References
Magnificent Frigate-bird (Fregata magnificens)	Common S Uncommon W	Yr	Y	Fish	Narcisse, pers. comm. Smith, pers. obs.
Turkey Vulture (Cathartes aura)	Common	Yr	Y	Carrion	Narcisse, pers. comm. Orians 1969
Black Vulture (Coragyps atratus)	Common	Yr	Y	Carrion	Robertson & Kushlan 1974 Orians 1969
Swallow-tailed Kite (Elanoides forficatus)	Common	S	Y	Snakes, lizards, frogs	Howell 1932 Snyder 19[illegible]
Sharp-shinned Hawk (Accipiter striatus)	Uncommon	W		Smaller passerines	Howell 1932
Cooper's Hawk (Accipiter cooperii)	Uncommon	Yr	Y	Larger passerines	Howell 1932
Red-tailed Hawk (Buteo jamaicensis)	Uncommon	Yr	Y	Small mammals, birds	Howell 1932
Red-shouldered Hawk (Buteo lineatus)	Common	Yr	Y	Snakes, frogs, lizards, insects	Howell 1932 Robertson & Kushlan 1974
Broad-winged Hawk (Buteo platypterus)	Uncommon	W		Insects, small mammals	Howell 1932
Swainson's Hawk (Buteo swainsoni)	Rare	W		Small mammals, grasshoppers	Howell 1932
Short-tailed Hawk (Buteo brachyurus)	Uncommon	W		Small birds	Howell 1932
Bald Eagle (Haliaeetus leucocephalus)	Rare-locally common (Fla. Bay)	Yr	Y	Fishes	Howell 1932
Marsh Hawk (Circus cyaneus)	Uncommon	W		Small mammals, shorebirds	Howell 1932
Osprey (Pandion haliaetus)	Common	Yr	Y	Fishes	Howell 1932
Peregrine Falcon (Falco peregrinus)	Very rare-locally common (Fla. Bay)	W		Waterfowl, shorebirds	Nisbet 1968 Ogden 1969 Howell 1932
Merlin (Falco columbarius)	Uncommon	W		Small birds, shorebirds	Howell 1932
American Kestrel (Falco sparverius)	Common	W		Insects	Howell 1932
Barn Owl (Tyto alba)	Uncommon	Yr	Y	Small mammals	Howell 1932
Great Horned Owl (Bubo virginianus)	Uncommon	Yr	Y	Waterfowl, small mammals	Howell 1932
Barred Owl (Strix varia)	Uncommon	Yr	Y	Small mammals, frogs, snakes	Howell 1932

ARBOREAL BIRDS

Common Name (Latin name)	Abundance	Season of Occurrence[a]	Nesting[a]	Food Habits	References
Mourning Dove (*Zenaidura macroura*)	Uncommon	Y	Y	Seeds	Emlen 1977
White-crowned Pigeon (*Columba leucocephala*)	Uncommon	Yr	Y	Berries, seeds, fruits	Howell 1932 Robertson & Kushlan 1974
Mangrove Cuckoo (*Coccyzus minor*)	Uncommon	Yr	Y	Caterpillars, mantids	Howell 1932 Ffrench 1966 Robertson & Kushlan 1974 Martin et al. 1951
Yellow-billed Cuckoo (*Coccyzus americanus*)	Common	S	Y	Caterpillars, beetles	Howell 1932 Ffrench 1966 Martin et al. 1951
Smooth-billed Ani (*Crotophaga ani*)	Rare	Yr	Y	Insects	Howell 1932 Ffrench 1966
Chuck-will's-widow (*Caprimulgus carolinensis*)	Uncommon	Yr	Y	Mosquitos, moths	Martin et al. 1951 Narcisse, pers. comm.
Common Flicker (*Colaptes auratus*)	Uncommon	Yr	Y	Ants, beetles, fruits in winter	Narcisse, pers. comm. Martin et al. 1951
Pileated Woodpecker (*Dryocopus pileatus*)	Uncommon	Yr	Y	Beetles, berries, fruits	Howell 1932 Robertson 1955 Robertson & Kushlan 1974
Red-bellied Woodpecker (*Melanerpes carolinus*)	Common	Yr	Y	Beetles, ants, grasshoppers, crickets	Narcisse, pers. comm. Martin et al. 1951
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	Rare	Yr	Y	Beetles, ants, grasshoppers, caterpillars	Narcisse, pers. comm. Martin et al. 1951
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	Uncommon	W,T		Beetles, ants, caterpillars	Narcisse, pers. comm. Martin et al. 1951
Hairy Woodpecker (*Picoides villosus*)	Rare	P		Insects, beetle larvae	Emlen 1977
Eastern Kingbird (*Tyrannus tyrannus*)	Uncommon	S,T	Y	Ants, wasps, grasshoppers	Narcisse, pers. comm. Martin et al. 1951
Gray Kingbird (*Tyrannus dominicensis*)	Common	S,T	Y	Bees, wasps, beetles, dragon	Howell 1932 Robertson & Kushlan 1974
Western Kingbird (*Tyrannus verticalus*)	Rare	W,T		Bees, wasps, grasshoppers	Narcisse, pers. comm. Martin et al. 1951
Great Crested Flycatcher (*Myiarchus crinitus*)	Uncommon (common S)	Yr	Y	Insects, berries	Howell 1932 Robertson 1955
Acadian Flycatcher (*Empidonax virescens*)	Rare	T		Small flying insects	Morton 1980
Eastern Phoebe (*Sayornis phoebe*)	Common	W		Bees, wasps, ants	Narcisse, pers. comm. Martin et al. 1951
Eastern Wood Pewee (*Contopus virens*)	Rare-uncommon	S,T		Bees, wasps, ants, moths	Narcisse, pers. comm. Howell 1932

ARBOREAL BIRDS (continued)

Common Name (Latin name)	Abundance	Season of Occurrence[a]	Nesting[a]	Food Habits	References
Barn Swallow (*Hirundo rustica*)	Locally common	W		Insects	Howell 1932 Bacon 1970
Blue Jay (*Cyanocitta cristata*)	Uncommon	Yr	Y	Grasshoppers, caterpillars, beetles	Narcisse, pers. comm. Martin et al. 1951
Tufted titmouse (*Parus bicolor*)	Very rare-rare	W		Caterpillars, wasps, bees	Howell 1932 Robertson & Kushlan 1974
Carolina Wren (*Thryothorus ludovicianus*)	Uncommon	Yr	Y	Ants, flies, millipeds	Narcisse, pers. comm. Martin et al. 1951
Mockingbird (*Mimus polyglottos*)	Abundant	Yr	Y	Fruits, berries	Robertson 1955
Catbird (*Dumetella carolinensis*)	Common	W,T		Fruits, insects	Narcisse, pers. comm. Martin et al. 1951
Brown Thrasher (*Toxostoma rufum*)	Uncommon	Yr	Y	Beetles	Narcisse, pers. comm. Martin et al. 1951
American Robin (*Turdus migratorius*)	Abundant	W		Worms, berries, insects	Narcisse, pers. comm. Martin et al.. 1951
Blue-gray Gnatcatcher (*Polioptila caerulea*)	Uncommon	W,T		Insects, especially Hymenopterans	Narcisse, pers. comm. Howell 1932
Ruby-crowned Kinglet (*Regulus calendula*)	Uncommon	W,T		Wasps, ants	Narcisse, pers. comm. Howell 1932
White-eyed Vireo (*Vireo griseus*)	Uncommon	S,T	Y	Butterflies, moths	Robertson 1955
Black-whiskered Vireo (*Vireo altiloquus*)	Uncommon	Yr	Y	Spiders, caterpillars	Howell 1932 Robertson & Kushlan, 1974
Red-eyed Vireo (*Vireo olivaceus*)	Uncommon	S,T	Y	Caterpillars, beetles	Narcisse, pers. comm. Howell, 1932
Yellow-throated Vireo (*Vireo flavifrons*)	Uncommon	W		Butterflies, moths,	Horton 1980
Black-and-White Warbler (*Mniotilta varia*)	Fairly common	W,T		Wood boring insects	Lack and Lack 1972 Keast 1980 Ogden 1969
Worm-eating Warbler (*Helmitheros vermivorus*)	Uncommon	W		Caterpillars, spiders	Ogden 1969 Kushlan, pers. comm.[c]
Prothonotary Warbler (*Protonotaria citrea*)	Uncommon	T		Insects	Pfrench, 1966 Russel 1980
Yellow-throated Warbler (*Dendroica dominica*)	Common	W		Beetles, moths, spiders	Horton 1980
Yellow Warbler (*Dendroica petechia*)	Common	yr	Y	Insects	Haverschmidt 1965 Pfrench 1966 Orians 1969 Terborgh & Faaborg 1980
Yellow-rumped Warbler (*Dendroica coronata*)	Abundant	W,T		Dipterans, bayberries	Narcisse, pers. comm.
Prairie Warbler (*Dendroica discolor*)	Uncommon	Yr	Y	Moths, beetles, flies	Lack & Lack 1972 Robertson & Kushlan 1974
Palm Warbler (*Dendroica palmarum*)	Abundant	W,T		Insects	Lack & Lack 1972 Emlen, 1977

ARBOREAL BIRDS (continued)

Common Name (Latin name)	Abundance	Season of Occurrence[a]	Nesting[a]	Food Habits	References
Blackpoll Warbler (*Dendroica striata*)	Uncommon	T		Insects	Ffrench 1966
Bay-breasted Warbler (*Dendroica castanea*)	Rare	T		Insects	Morton 1980
Black-throated Green Warbler (*Dendroica virens*)	Uncommon	W		Aphids, leaf-rollers, and other insects	Ogden 1969 Kushlan, pers. comm.
Chestnut-sided Warbler (*Dendroica pensylvanica*)	Rare	T		Insects	Morton 1980
Cape May Warbler (*Dendroica tigrina*)	Uncommon Common	W T			Ogden 1969
Black-throated Gray Warbler (*Dendroica nigrescens*)	Rare	W		Insects	Ogden 1969 Kushlan, pers. comm. Hutto 1980
Black-throated Blue Warbler (*Dendroica caerulescens*)	Uncommon Common	W T		Beetles, flies, ants	Kushlan, pers. comm. Ogden 1969
Northern Waterthrush (*Seiurus noveboracensis*)	Abundant Rare	T W		Insects	Schwartz 1964 Ffrench 1966 Bacon 1970 Russell 1980
Yellowthroat (*Geothlypus trichas*)	Common	Yr	Y	Grasshoppers, crickets, ants, wasps	Narcisse, pers. comm. Howell 1932 Lack & Lack 1972
American Redstart (*Setophaga ruticilla*)	Common	T		Caterpillars	Bennett 1980 Ffrench 1966 Bacon 1970
Tennessee Warbler (*Vermivora peregrina*)	Uncommon	T		Insects	Morton 1980
Nasheville Warbler (*Vermivora ruficapilla*)	Rare	T		Insects	Hutto 1980
Orange-crowned Warbler (*Vermivora celata*)	Common	W		Insects	Hutto 1980
Golden-winged Warbler (*Vermivora chrysoptera*)	Rare	T		Insects	Morton 1980
Northern Parula (*Parula americana*)	Common	W		Hymenoptera	Lack and Lack 1972
Ovenbird (*Seiurus aurocapillus*)	Common	W		Beetles, crickets, grasshoppers	Lack and Lack 1972
Kentucky Warbler (*Oporornis formosus*)	Rare-uncommon	T		Beetles, caterpillars, ants	Morton 1980
Mourning Warbler (*Oporornis philadelphia*)	Rare	T		Insects	Morton 1980
Yellow-breasted Chat (*Icteria virens*)	Common	W		Hymenoptera	Hutto 1980

ARBOREAL BIRDS (concluded)

Common Name (Latin name)	Abundance	Season of Occurrence[a]	Nesting[a]	Food Habits	References
Wilson's Warbler (Wilsonia pusilla)	Rare-uncommon	T		Insects	Hutto 1980 Ramos and Warner 1980
Red-winged Blackbird (Agelaius phoenicaus)	Common	Yr		Seeds, insects	Howell 1932 Robertson 1955
Boat-tailed Grackle (Quiscalus major)	Uncommon	Yr	Y	Crayfish, crabs, shrimp	Robertson 1955 Girard & Taylor 1979
Common Grackle (Quiscalus quiscula)	Uncommon	Yr	Y	Insects, caterpillars	Howell 1932 Robertson 1955
Cardinal (Cardinalis cardinalis)	Common	Yr	Y	Insects, seeds	Robertson 1955
Orchard Oriole (Icterus spurius)	Rare	T		Grasshoppers, beetles	Morton 1980
Indigo Bunting (Passerina cyanea)	Uncommon	W,T		Grasshoppers, caterpillars	Narcisse, pers. comm. Howell 1932
Summer Tanager (Piranga rubra)	Uncommon	T		Hymenoptera	Morton 1980
Dickcissel (Spiza americana)	Uncommon	W,T		Caterpillars, beetles	Bacon 1970 Martin et al. 1951
Rufous-sided Towhee (Pipilo erythrophthalmus)	Common	Yr	Y	Caterpillars, bayberries, fruits	Narcisse, pers. comm. Howell 1932
Swamp Sparrow (Melospiza georgiana)	Common	W,T		Ants, flies, seeds	Narcisse, pers. comm. Howell 1932

[a] Yr = year round resident
S = summer resident
W = winter resident
T = transient, present only during spring and fall migration
Y = species breeds in mangroves

[b] L. Narcisse, R.N. "Ding" Darling Fed. Wildlife Refuge, Sanibel Island, Fla. (1981).

[c] J.A. Kushlan, So. Fla. Res. Ctr., Everglades Natl. Park, Homestead, Fla.

APPENDIX E. Mammals of south Florida mangrove swamps.

MAMMALS OF FLORIDA MANGROVES

Species	Status	Food Habits
Virginia Opossum (*Didelphis virginiana*)	Abundant	Fruits, berries, insects, frogs, snakes, small birds and mammals
Short-tailed Shrew (*Blarina brevicauda*)	Uncommon	Insects
Marsh Rabbit (*Sylvilagus palustris*)	Abundant	Emergent aquatics
Gray Squirrel (*Sciurus carolinensis*)	Occasional	Fruits, berries, mast, seeds
Fox Squirrel (*Sciurus niger*)	Rare	Fruits, berries, mast
Marsh Rice Rat (*Oryzomys palustris*)	Uncommon	Seeds of emergent plants, insects, crabs
Cudjoe Key Rice Rat (*Oryzomys argentatus*)	Rare	Seeds, insects, crabs
Cotton Rat (*Sigmodon hispidus*)	Abundant	Sedges, grasses, crayfish, crabs, insects
Gray Fox (*Urocyon cinereoargenteus*)	Uncommon	Small mammals, birds
Black Bear (*Ursus americanus*)	Rare	Fruits, berries, fish, mice
Raccoon (*Procyon lotor*)	Abundant	Crayfish, frogs, fish
Mink (*Mustela vison*)	Rare	Small mammals, fish, frogs, snakes, aquatic insects
Striped Skunk (*Mephitis mephitis*)	Common	Bird eggs and young frogs, mice, larger invertebrates
River Otter (*Lutra canadensis*)	Uncommon	Crayfish, fish, mussels

MAMMALS OF FLORIDA MANGROVES (concluded)

Species	Status	Food Habits
Panther (*Felis concolor*)	Very rare	Deer, rabbits, mice, birds
Bobcat (*Felis rufus*)	Common	Rabbits, squirrels, birds
White-tailed Deer (*Odocoileus virginianus*)	Common	Emergent aquatics, nuts, acorns, occasionally mangrove leaves
Key Deer (*O.v. clavium*)	Common on certain Florida Keys (no longer on mainland)	Emergent aquatics and other vegetation
Black Rat (*Rattus rattus*)	Common	
Bottle-nosed Dolphin (*Tursiops truncatus*)	Uncommon	Fish
West Indian Manatee (*Trichechus manatus*)	Uncommon	Submerged aquatics, *Zostera*, *Ruppia*, *Halodule*, *Syringodium*, *Cymodocea* , *Thalassia*

References: Layne 1974; Hamilton and Whittaker 1979; L. Narcisse, R.N. "Ding" Darling Fed. Wildlife Refuge, Sanibel Island, Fla.; personal communication.

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16. Abstract (Limit: 200 words)

A detailed description is given of the community structure and ecosystem processes of the mangrove forests of south Florida. This description is based upon a compilation of data and hypotheses from published and unpublished sources.

Information covered ranges from details of mangrove distribution, primary production, and diseases to aspects of reproduction, biomass partitioning, and adaptations to stress. Mangrove ecosystems are considered in terms of zonation, succession, litter fall and decomposition, carbon export, and energy flow.

Most of the components of mangrove communities are cataloged and discussed; these include microorganisms, plants other than mangroves, invertebrates, fishes, reptiles, amphibians, birds, and mammals.

Finally, two sections summarize the value of mangrove ecosystems to man and present ways to manage this type of habitat. It is concluded that mangrove forests, which cover between 430,000 and 500,000 acres (174,000 - 202,000 ha) in Florida, are a resource of great value and should be protected and preserved wherever possible.

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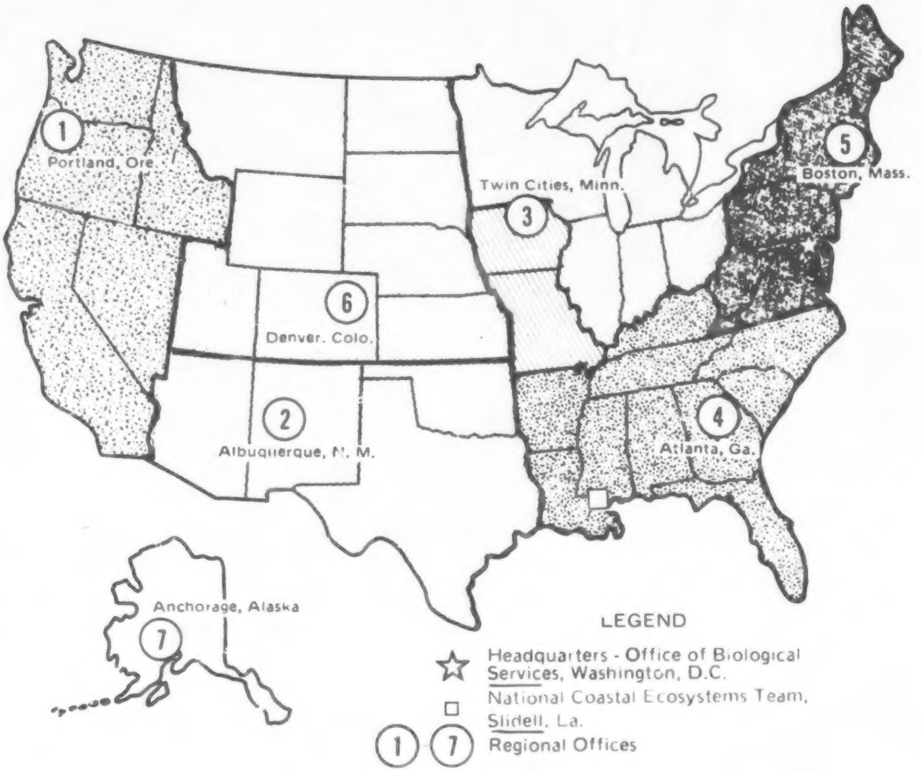
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